

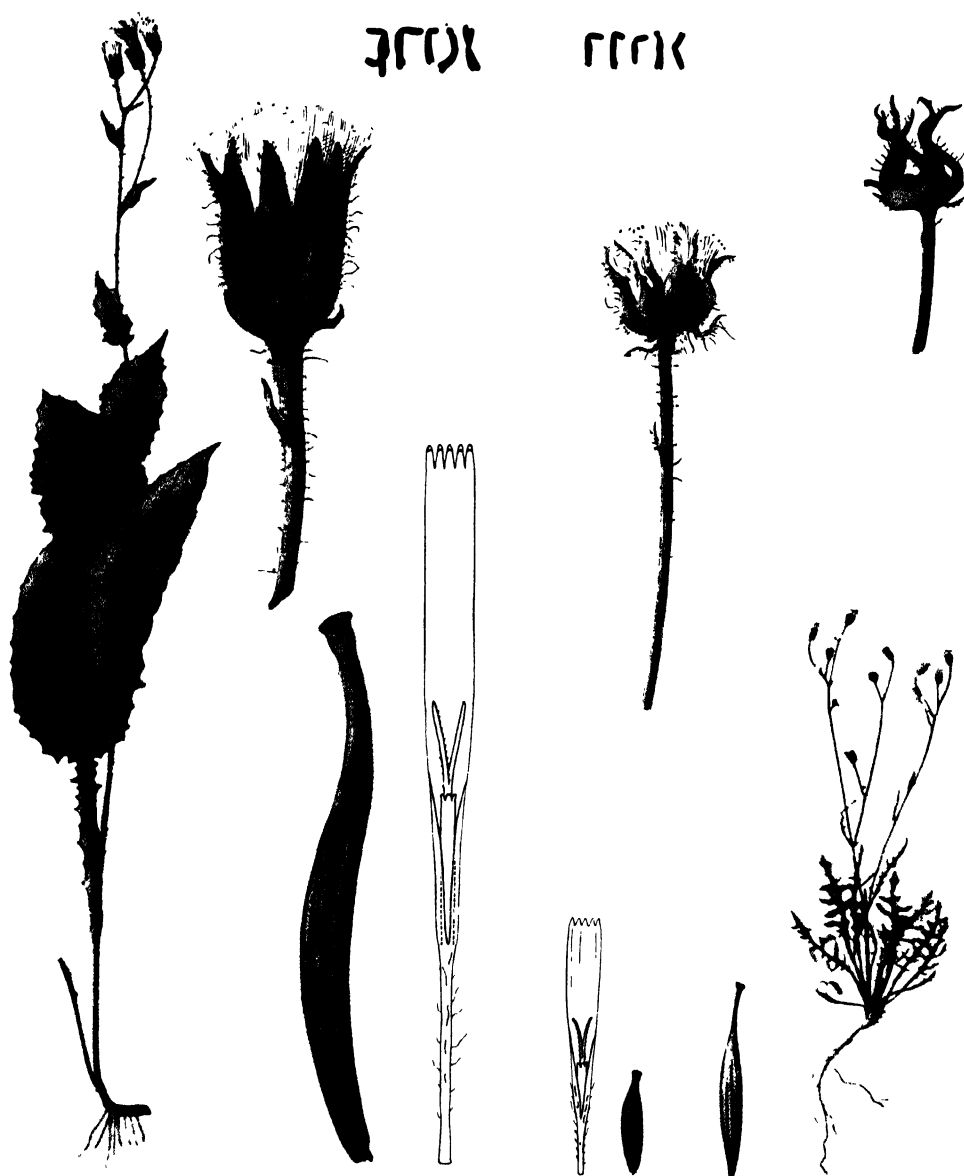


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Crepis sibirica (left), the most primitive, and *C. suberosa* (right), the most advanced species in the genus having 5 pairs of chromosomes. *C. sibirica* is a widespread perennial species of northern Eurasia; it is a typical cryptophyte with a rhizome. (Note the large lyrate leaves, the few large flower heads, especially the involuere with many large bracts, which remain unchanged at maturity, and the comparatively large size of the individual floret and the columnar achene.) *C. suberosa* is a polymorphic annual species of Algeria. The plant shown above is subsp. *typica* which occurs only in a small area in the littoral sand dunes; whereas subsp. *arcuosa*, which is represented above by the finely beaked achene, occurs more widely in the arid uplands. (Note the branching taproot, the smaller dissected leaves, the numerous small heads, the involuere with few small bracts and with basal thickening at maturity, the comparatively small floret and achene, and the presence of a beak on the achene.) All to the same scales.

THE GENUS CREPIS

PART ONE

The Taxonomy, Phylogeny, Distribution, and Evolution of Crepis

BY

ERNEST BROWN BABCOCK

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Part One

**THE TAXONOMY, PHYLOGENY, DISTRIBUTION,
AND EVOLUTION OF CREPIS**

Part One of this work embraces pages i-xii + 1-198, in which are included frontispiece, plate 1, text figures 1 to 11 and A-D, and tables 1 to 12.

Part Two (University of California Publications in Botany, Volume 22) subtitled

Systematic Treatment

embraces pages i-x + 199-1030, in which are included plates 2 to 36, text figures 12 to 305, and tables 13 to 19. The treatment of the 27 sections, giving detailed data on the 196 species of the genus, is introduced by subdivisions entitled general plan, descriptions, abbreviations and citations, history, diagnosis, and description of the genus, diagnosis of the sections, and key to the sections. Following the sections are named hybrids, species not sufficiently known, excluded names, and indexes.

CHAPTER 1

HISTORY OF THE INVESTIGATIONS, WITH RESULTS AND CONCLUSIONS OF SIGNIFICANCE FOR SYSTEMATICS

EARLIEST STUDIES, 1915-1922

THE INVESTIGATIONS which led to the writing of this monograph had their inception in 1915 when the published reports of Rosenberg (1909a) and Digby (1914) that *Crepis capillaris* has 3 pairs of chromosomes in its somatic cells, and of Juel (1905) and Rosenberg (1909a) that *C. tectorum* has 4 pairs of somatic chromosomes, were brought to the attention of the author. The importance of the low number of chromosomes in *Drosophila melanogaster* in expediting the research which led to the epoch-making discoveries of Morgan (1915) suggested the possible value of these species of *Crepis* for genetic investigations. Seeds of the two species mentioned above were obtained from several botanic gardens and from the wild; and extensive garden cultures were grown in 1917 and 1918 from which many selections were made for the study of variable characters. At the same time, attempts were made to produce hybrids between these two species. The results of these early studies are mentioned below under genetic research.

In 1918 these *Crepis* investigations were recognized by the California Agricultural Experiment Station as a major project of the Division of Genetics. Since that time, funds have been allocated annually for the maintenance of the project. These funds, together with other funds mentioned below under acknowledgments, have made possible the continuity of research which has resulted in many publications, some of which are listed among the references at the end of this volume, and in the preparation and publication of this monograph. The first mention of the *Crepis* work in the annual reports of the California Agricultural Experiment Station is found in the report for the year ending June 30, 1920 (cf. Babcock, 1920-1932).

This continuous support of fundamental research on a group of noneconomic plants throughout a period of twenty-five years by an agricultural institution reveals a far-sighted policy on the part of the administration of the California Agricultural Experiment Station. It is the hope of the author that the results of these investigations, as summarized by this monograph, will be found to justify such a policy.

Although the genus *Crepis* includes no cultivated crop plant, some of the species are of value for one purpose or another. Many species of *Crepis* are valuable as wild forage for cattle and sheep. This is certainly true of the native western American *Crepis* and it holds good for several species in the Mediterranean region. The fact that *C. divaricata* of Madeira is now almost extinct is undoubtedly due to its use as a forage plant for goats and pigs. Furthermore, some of the Old World species are used by the country people as green salads and it is not unlikely that some of them could be developed into useful cultivated salad plants. In *C. palaestina*, for example, cultivated strains exhibited wide differences in leaf size, amount of pubescence, and degree of bitterness when chewed, and some of these strains seemed fairly promising. As an ornamental, *Crepis rubra* has long been grown in Old World flower gardens. Another pink-flowered species, *C. incana*, is a desirable plant for rockeries. Some of the perennial and biennial species have showy yellow flowers, and one of these, *C. chondrilloides*, is interesting because of its remarkable laciniate leaves. At least one species seems to be of some importance as a plant producing medicinal

poison. *Crepis latialis* of Italy is reported to be extremely poisonous and to be of value in certain heart ailments (see Part II, p. 446). Finally, two common Old World weeds, *Crepis capillaris* (*C. virens*) and *C. vesicaria* subsp. *taraxacifolia* (*C. taraxacifolia*), as well as the rare alpine species, *C. incana*, have recently been found to yield a substance which inhibits the growth of *Staphylococcus aureus* (Osborn, 1943). The evidence reported by Osborn has shown that antibacterial substances are present in very many green plants. The investigation of *C. vesicaria taraxacifolia* by Heatley (1944) shows that the substance "crepin" is antibiotic, since human leucocytes became sluggish but survived for two hours in a solution of 1 in 4,500,000. Yet even at 1 in 4,500, the strongest solution tested, a few cells were alive after two hours, a rather remarkable fact. Crepin also inhibits the growth of *Streptococcus pyogenes* and several other bacteria. It does not occur in free form but as an antibiotically inactive precursor. The agent, presumably an enzyme which activates the precursor, appeared to be confined to the yellow ligules of the florets and, to a much smaller extent, to the roots; whereas the substrate from which crepin is liberated occurs, except for the stem and leaves, in most parts of the plant. Crepin crystallizes from alcoholic solutions in three forms. The yield is small, rarely exceeding 100 milligrams of pure crystals per kilogram of fresh starting material. In this connection it may be worth noting that *C. latialis* might possibly yield crepin in much larger quantities.

The encouragement derived from the earliest studies and efforts in interspecific hybridization led to a definite plan for assembling as many as possible of the known species of *Crepis* in living condition. As a result of extensive correspondence with the directors of botanic gardens throughout the world and with botanical collectors in many countries, the collection of living species increased rapidly. In 1920, 22 species were under cultivation at Berkeley; and in 1921, 29 species were grown. Since that time the number has increased until a total of 113 species of *Crepis* have been cultivated at Berkeley. A few of these species could be grown for only a short time or were represented by only one or two seedlings; but the greater part of them were under cultivation and observation for several years.

In 1920 the author published a paper (Babcock, 1920) intended to call attention to the promising features of *Crepis* as an object of genetic investigation, and at the same time point out the technical difficulties involved in hybridizing such plants. The hope that others would be encouraged to undertake similar research on this group of plants, so that through coöperation more rapid progress might be made, was richly rewarded by the outstanding work of Dr. M. S. Navashin of Moscow. Later, Navashin spent nearly two years at Berkeley collaborating with the present author.

TAXONOMIC STUDIES, 1923-1942

The growing list of accessions of species of *Crepis* and allied genera in the collection of living plants brought to light more and more a state of nomenclatural confusion which made us realize that a thorough revision of the genus was imperative. It was realized that such an undertaking would require a number of years; but it must be admitted that, had the author then appreciated the magnitude of the task, it is doubtful whether he would have undertaken it.

Herbarium studies.—After going over the collection of *Crepis* material then in the University of California Herbarium and reviewing as much as possible of the literature pertaining to the list of species referred to *Crepis* in Index Kewensis, the author spent the year 1924-1925 working in other herbaria. Several months were spent in the eastern United States with headquarters at the Gray Herbarium. Next, a number of European herbaria were visited for the purpose of studying

types, critical material, and as many other specimens as possible, as well as for the purpose of consulting references not available in America. In Berkeley, herbarium studies were continued by means of borrowed specimens (see acknowledgments, p. 29). More than 5,400 herbarium specimens are cited in Part II, and probably as many more have been examined but not cited. In addition, several thousand plants have been observed both in the wild and under cultivation and hundreds have been used in experimentation. Many valuable hints concerning interspecific relationships have come to light through observation of cultivated specimens during various stages in ontogeny.

Author's collections.—The first collections made by the author were in 1925 while on a brief trip through eastern California, Nevada, and southeastern Oregon with Dr. Harvey M. Hall, who was making collections for use in connection with his transplant experiments. Only a few species of *Crepis* were obtained on this trip, particularly *C. occidentalis*, *C. modocensis*, and *C. runcinata*. In 1926 an expedition was made in company with Dr. J. L. Collins, who was then a member of the Division of Genetics, through northern California, central and eastern Oregon and Washington, and western Idaho. Eight different *Crepis* species were obtained, including living material of *C. barbiger*, *C. atribarba*, and several variants of *C. runcinata* subsp. *hispidulosa*. In 1927 an 8,000-mile expedition was made in company with Dr. D. B. Goddard, then of the Department of Botany, University of California, through California, Arizona, New Mexico, Colorado, Wyoming, Yellowstone National Park, Utah, and Nevada. Herbarium specimens and living material of *C. occidentalis*, *C. intermedia*, *C. atribarba*, and numerous forms of *C. runcinata* were obtained. The last-mentioned material proved valuable in checking on the synonymy of this highly polymorphic species. In 1928 an expedition was made through the northern Sierra Nevada from Truckee to Feather River Canyon and out through Plumas and Tehama counties. Seven species, including many forms, were obtained on this trip, and Dr. Navashin preserved young flower heads for cytological study. In 1930 the author made a five months' expedition in the Mediterranean region for the purpose of collecting living material of *Crepis* species. The itinerary included Madeira, Portugal, Spain, Morocco, Algeria, Tunisia, Sicily, Italy, Greece, Crete, Corsica, Majorca, and the southern Pyrenees. Thirty-three species or subspecies were obtained, including roots or seeds of most of them. Through the kind coöperation of the Quarantine Service of the United States Department of Agriculture, the several packages of roots collected on this expedition were forwarded to California promptly, making it possible for each species to be brought into cultivation and to be examined cytologically. Through the kindness of acquaintances made in Algiers (Dr. René Maire), in Greece (M. Guiol and Miss S. P. Topali), and in Spain (Sr. Ramon Sala and, through him, Dr. P. Font Quer and others), additional very valuable material, including several new species, were received in later years. In 1931, 1932, and 1934 short excursions were made in California and Washington where other material of the American species was obtained. In 1936 another expedition was made in the northern Sierra Nevada in company with Dr. G. L. Stebbins, Jr., who was then associated with me in the *Crepis* investigations on a grant from the Rockefeller Foundation. Detailed field studies, including castration experiments and cytological preparations, were made on the *Crepis* species found in Sierra Valley, and collections were made from there northward into the Feather River Canyon. Other sources of living material of *Crepis* are listed below under acknowledgments.

COMPARATIVE MORPHOLOGY THE BASIS OF PHYLOGENY

It is important at the outset to make perfectly clear that the systematic treatment of *Crepis* presented in this monograph rests primarily on comparative morphology. Unfortunate misunderstandings have arisen through misinterpretation of some of the earlier publications on the relations between the chromosomes and phylogeny in this genus. It has even been stated that our phylogenetic conclusions were based on chromosome number alone. Nothing could be further from the truth. In all of our earlier studies, attempts were made to coördinate the evidence from cytology and genetics with the best existing taxonomic treatments of the genus as a whole, found in de Candolle's *Prodromus*, Bentham and Hooker's *Genera Plantarum*, and Engler and Prantl's *Pflanzenfamilien*. These classical works were of course based exclusively on morphology. At the same time, more critical study of morphological details soon revealed serious discrepancies in those older attempts at a taxonomic treatment of this genus; for example, the recognition of *Crepis pulchra* and *C. palaestina* as two monotypic genera, *Phaegasium* and *Cymboseris*. It must be admitted that it was only after finding that the chromosomes of the two species were practically identical in number, size, and shape that a more critical examination of their morphology was made. This evidence on the chromosomes was supplemented by the demonstration that the two species cross readily and the F_1 hybrids are fairly fertile. Then, it was found that the chief reason for the misconception of the older taxonomists was their overemphasis on differences in shape of the fruits. It was also found that *C. pulchra typica* itself is variable in the shape of its marginal achenes (those adjacent to the inner involucre bracts) and that in some forms of this subspecies the marginal achenes are strongly compressed and resemble those of *C. palaestina*. In this monograph, therefore, these two species will be found in the same subgroup of the same section which bears the name of the older of the two monotypic genera mentioned above, *Phaegasium*. A great deal of the confusion which has arisen in the early taxonomic works on *Crepis* has resulted from such overemphasis on one or a few differences and from failure to recognize fundamental resemblances. This will suffice to illustrate how the evidence from comparative morphology, cytology, and genetics has been combined in the determination of interspecific relationships in *Crepis*.

The question of the relative importance of the various criteria of taxonomic and phylogenetic relations may still be open to debate. Smith (1933), in his cytotaxonomic treatise on *Primula* states: "I believe that the last word lies with the morphology. But I can record without hesitation my obligations to the cytologist." What is true of cytology may also be true, and in many instances to a greater degree, of genetics, experimental taxonomy, and geographic distribution. But it must be emphasized that, up to the present time, less than 60 per cent of all the known species of *Crepis* have been brought into cultivation and thus been available for cytologic and genetic research. Comparative morphology, therefore, is of necessity the primary basis of classification in this monograph.

RESEARCH ON THE CHROMOSOMES, 1918-1942

In order to give the reader a concrete notion of the morphological contrasts between the most primitive and most advanced types of *Crepis* species, one of each is shown in the frontispiece, in which all objects are reproduced to the same scales. *Crepis sibirica*, with 5 pairs of chromosomes, has primitive morphological characteristics. It is a strong perennial with horizontal rhizome, large lyrate leaves, few large heads with very large florets and achenes, and the involucre consists of many

large bracts which remain unchanged at maturity. *C. suberostris* subsp. *typica* represents the most advanced species in the genus having 5 pairs of chromosomes. It is a short-lived annual of the littoral sand dunes of Algeria. Its leaves are dissected, its flower heads are numerous and small, and the specialized involucre, having only a few small bracts, becomes much thickened at maturity. These striking morphological and physiological differences in the two species are the result of evolution within a group of *Crepis* species having the same chromosome number.

Two species having different chromosome numbers are also illustrated (figs. A and B). The differences in size and habit of the plant, in size of the heads, florets, fruits, etc., are so obvious it seems hardly necessary to point them out. The primitive species, *C. geracioides*, is a montane perennial which is endemic in the southern Balkan Peninsula. The advanced species, *C. senecioides*, is a precocious desert annual which has been collected at a number of stations scattered along the Egyptian-Tunisian littoral. Since, on morphological grounds, it is the most advanced species in the genus, it has been used to illustrate the extreme reduction in size which has accompanied development of the annual habit, the extreme precocity, and the remarkable longevity of the tiny achenes, all of which adapt it so well to desert conditions. The fact that these two species, which represent the earliest and latest stages in a very long developmental history, now exist on opposite sides of the Mediterranean Sea, which is only some 600 kilometers (400 miles) wide in this region, is sufficient to pique one's curiosity concerning whence and how they came to be there. The present volume attempts to synthesize the evidence and to derive the most probable hypothesis explaining the present distribution of *Crepis*.

Progress in the studies on the chromosomes of *Crepis* was marked by the publication of papers by Rosenberg (1918, 1920), Navashin (1925, 1926, 1927), Mann (1925), Babcock and Mann Lesley (1926), Hollingshead and Babcock (1930), Babcock and Cameron (1934), Babcock, Stebbins, and Jenkins (1942), and Babcock and Jenkins (1943). All of these papers except the last two are reviewed either by Babcock and Navashin (1930) or by Babcock (1942). Following is a general summary of the information available up to the present, arranged topically.

Chromosome numbers.—On the basis of chromosome numbers alone, this genus consists of two different groups of species: the American species, which have, excluding *C. nana* and *C. elegans* of section 12, the base number, $x=11$, and the Old World species, none of which has this number. These 10 polyploid American species are discussed below (see p. 22 and Part II, sec. 15). Of the other 103 species which have been studied cytologically, only 6 are polyploids. These consist of 3 tetraploids with $x=4$ and 3 octoploids with $x=5$. The remaining 97 species are diploids, which are classified, according to their haploid numbers, as follows: 3 species with $n=3$, 58 with $n=4$, 19 with $n=5$, 14 with $n=6$, and 3 with $n=7$.

The 3-paired species include the well-known *C. capillaris*, along with *C. fuliginosa* and *C. Zacintha*. It is improbable that many more *Crepis* species having as few as 3 pairs of chromosomes will be discovered. Apparently, $n=3$ represents an end point in an evolutionary process resulting in reduction in chromosome number. It is noteworthy that these three species, on the basis of comparative morphology, are among the most advanced in the genus.

The three species with $n=7$, together with four others classed with them because of morphological similarity, comprise the section *Ixeridopsis* which is not among the most primitive sections of the genus. It was suggested by Babcock, Stebbins, and Jenkins (1937) that there is a close genetic connection between these 7-paired *Crepis* species and the 7-paired *Ixeris alpicola* which came about as a result of hybridization between the two genera when they were in a formative period, a



Fig. A. *Crepis geracioides*: a, plant, $\times \frac{1}{2}$; b, flower head, $\times 2$; c, a floret lacking the ovary, $\times 4$; d, anther tube slit and opened out, $\times 8$; e, detail of anther appendages, $\times 32$; f, g, 2 achenes and a pappus seta from each, $\times 8$; h, h', 2 inner involucre bracts showing outer and inner faces, respectively, $\times 4$; i, haploid set of chromosomes, $\times 1500$.



Fig. B. *Crepis senecioides*: a-c and k, plants and parts, $\times \frac{1}{2}$; d, m, florets lacking the ovary, $\times 4$; e, n, anther tubes slit and opened out, $\times 8$; f, o, details of anther appendages, $\times 32$; g, h, p, q, achenes and single pappus setae, $\times 8$; r, haploid set of chromosomes, $\times 1500$.

suggestion compatible with the morphology and geographic distribution of the two groups. This section, therefore, need not be considered further in connection with the history of the main part of the genus.

The remaining diploid species have $n = 4, 5$, or 6 , with 4 greatly predominating. However, the nine most primitive species in the genus, as determined from both plant morphology and chromosome morphology, have either 6 or 5 pairs of chromosomes. The most primitive chromosome numbers in *Crepis* are 6 and 5 . The great predominance of the number 4 means simply that reduction in chromosome number has accompanied differentiation and speciation along with morphological re-

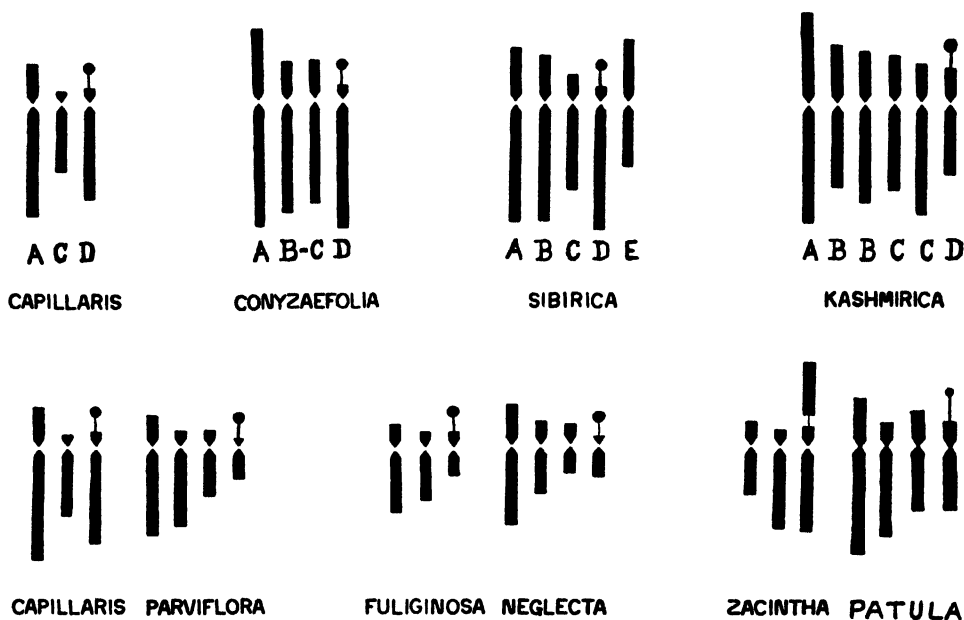


Fig. 1, upper row. Idiograms of four species of *Crepis*. Capital letters indicate the various chromosome types. In *C. conyzaeifolia* it is impossible to distinguish between the B and C chromosomes from their gross appearance in somatic cells. In *C. kashmirica*, with 6 pairs of chromosomes, no E chromosome is present, but there are two each of B and C types. Lower row. Idiograms of the three 3-paired species and the most closely related species of each.

duction and specialization in this genus. Many variations in the typical diploid chromosome numbers have been reported. These are reviewed by Babcock (1942, pp. 148-149).

Karyotypes.—The term karyotype is used here to designate the gross structure of the chromosomes, following Levitsky (1924). A diagrammatic representation of a haploid or basic chromosome set is an idiogram. The original work of Navashin (1925) on *Crepis* karyotypes dealt with 3-paired, 4-paired, and 5-paired species. For purposes of comparison he labeled the members of the idiograms with capital letters, a device still used in describing *Crepis* karyotypes. The complement of a species with $n = 5$ was found to consist of 4 pairs, with a subterminal spindle-fiber attachment or centromere, whereas the fifth pair has a median or nearly median centromere. The one (of the four with subterminal centromere) having the longest proximal arm was designated A, that with the next longest proximal arm was usually B, that with the next longest proximal arm was usually C, and the D chromosome has an extremely short proximal arm or "head" bearing a satellite. The medianly con-

stricted member was labeled E. The idiogram of *Crepis sibirica*, shown in figure 1, has these 5 members. As a matter of fact, the distinctions between type B and type C, as well as between type B and type A, are sometimes arbitrary; but in many 5-paired species it is easy to distinguish definitely between the 5 members of the karyotype. In the 4-paired species studied by Navashin the E chromosome was always lacking; and this has been found to be generally true of the 4-paired species of *Crepis* with a few exceptions, such as *C. oporinoides* of section 10 (Part II, fig. 112), the species of section 19 (Part II, figs. 192–201), in which the A chromosome has a median centromere, and *C. neglecta*, *C. corymbosa*, and *C. Suffreniana* of section 24 (Part II, figs. 246, 247, 251). In the idiogram of *C. conyzaefolia*, shown in figure 1, it is very difficult to distinguish between the B and C chromosomes by the length of the proximal arms, and their distal arms are nearly the same length. In a primitive 6-paired species, such as *C. kashmirica*, 4 of the chromosomes fall into the B or C classes and there is no E chromosome present. Thus, the original scheme of Navashin requires some modifications even for the purpose of labeling the chromosomes according to their gross appearance.

In *C. capillaris* (fig. 1) there are no chromosomes corresponding in appearance to the B and E types; therefore, the three elements present were labeled A, C, and D by Navashin. But, if it is assumed that the 3-paired species were derived from 4-paired ancestors (a necessary assumption if 3 is an end point in a progressively reductional series), then the letters used to designate the three elements may not represent the same chromatin material as in its close relative, *C. parviflora*, or their common ancestor (fig. 1, lower row). It has not yet been possible to compare the chromosomes of *C. capillaris* and *C. parviflora* by means of cytogenetic research on their hybrid; but in *C. fuliginosa* and its nearest relative, *C. neglecta*, this has been done by Tobgy (1943), with the result that it can be stated definitely that the C chromosome of *C. neglecta* is missing, as a separate chromosome, in *C. fuliginosa*, although part of its component material is now present in the B chromosome of this species. In other words, we are certain that the A, B, and D chromosomes of *C. fuliginosa*, considered as entities, are homologous with the A, B, and D chromosomes of *C. neglecta*. This important discovery is discussed below, under karyotype evolution. When the chromosomes of *C. Zacintha* and its closest relative, *C. patula*, are compared (fig. 1), the difficulty of homologizing the chromosomes of the two species from their gross appearance is obvious. Thus, it becomes clear that, although labeling the chromosomes of various species has been a useful device for certain purposes, it must be clearly understood, as Navashin and Gerassimova (1935, 1936) have pointed out, that homologizing the chromosomes of different species solely on the basis of their gross appearance is likely to lead to confusion.

Chromosomes and phylogeny.—The phylogenetic significance of chromosome number, size, and shape can be interpreted only in relation to or with aid of other criteria. In the first effort to synthesize the evidence from taxonomy and cytology (Babcock and Mann Lesley, 1926), thirty-three species were considered, including *Aetheorrhiza bulbosa* and two species of *Youngia* which are now excluded from *Crepis*. Because certain changes in the sections of Hoffmann (in Engler and Prantl's *Pflanzenfamilien*) were found to be necessary in order to coördinate the data on chromosome number and size, a tentative new classification by sections was proposed. Hollingshead and Babcock (1930) reported on sixty-five species, including one species of *Youngia* which is now excluded. Eight of these species were restricted to North America. Four major subgeneric groups, Paleya, Barkhausia, Catonia, and Eucrepis, were recognized, and a tentative phylogenetic scheme was drawn up with Paleya (*C. albidia*) assumed to represent the ancestral form. Seventeen sub-

groups or sections were recognized on the combined evidence from comparative morphology and the chromosomes. One of these comprised seven American species, with somatic chromosome numbers ranging from 22 to 88. It was suggested that they originated from hybridization between Asiatic species having 4 and 7 pairs or 5 and 6 pairs of chromosomes, followed by amphidiploidy. The general conclusion was reached that, in each section of the genus, morphologically similar species have similar chromosomes and there is a fairly close parallelism in *Crepis* between number and morphology of the chromosomes and phylogenetic relationship.

Four years later, Babcock and Cameron (1934), after comparing the karyotypes of 108 species and considering the evidence on relationship provided by other criteria, concluded as follows: (1) morphologically similar species have similar chromosomes; (2) similarity in chromosome types and in details of size and shape is an index of phylogenetic relationship (when used, of course, in connection with other criteria); (3) both increase and decrease in chromosome size have occurred in the evolution of the genus; (4) a general tendency toward reduction in size of the chromosomes exists concurrently with reduction in size of the plant and reduction or specialization of parts; (5) many changes have taken place in chromosome shape, as determined by relative length of the arms, and by these differences chromosomes of the same types from different species can be identified in hybrids; (6) this fact makes it possible, by analysis of the haploid karyotype, to determine the mode of origin of certain species; and (7) chromosome number and morphology are taxonomic criteria of great value in this genus. But the chromosomes must be used in connection with other available criteria, such as comparative morphology, genetic data, and geographic distribution. Certainly absolute identity of the chromosomes cannot be set up as of paramount importance in the classification of species, for species are known in which different forms exhibit differences in number, size, or shape of the chromosomes. The genus is still evolving and visible changes in the chromosomes are part of the process. Many alterations in specific karyotypes have been induced experimentally and some have arisen spontaneously. These are discussed below (pp. 18-20).

Karyotype evolution.—It has been pointed out (Babcock, Stebbins, and Jenkins, 1942) that there are distinct evolutionary trends in the karyotype diversity in *Crepis* and that these karyotype changes may be summarized under a number of distinct heads.

1) *A progressive decrease in the basic chromosomal number* is the most outstanding karyotype change occurring in the genus *Crepis*. In spite of the fact that most of the species have a basic number of 4, the morphologic and geographic evidence indicates that the primitive number is 6, and those species with 5, 4, and 3 as the haploid number are definitely derived. There are a few exceptions to this progressive decrease in chromosome number which involve either polyploidy or hybridization or both.

2) *Polyploidy* is largely confined to the American species, in which, together with apomictic reproduction, it has resulted in a great diversity of forms, i.e., in large species complexes. In the rest of the genus, doubling of the chromosome number, although having occurred on several occasions, has, on the whole, played a relatively minor role.

3) *An increase in asymmetry* is manifested in two ways: (1) a tendency exists for the more advanced species to have karyotypes made up of chromosomes of unequal lengths; and (2) the more advanced species have chromosomes with a more terminally situated centromere, which leads to a chromosome with one arm longer than the other.

IDIOGRAMS SHOWING KARYOTYPE EVOLUTION IN CREPIS REDUCTION IN NUMBER, TOTAL LENGTH AND SYMMETRY OF THE CHROMOSOMES

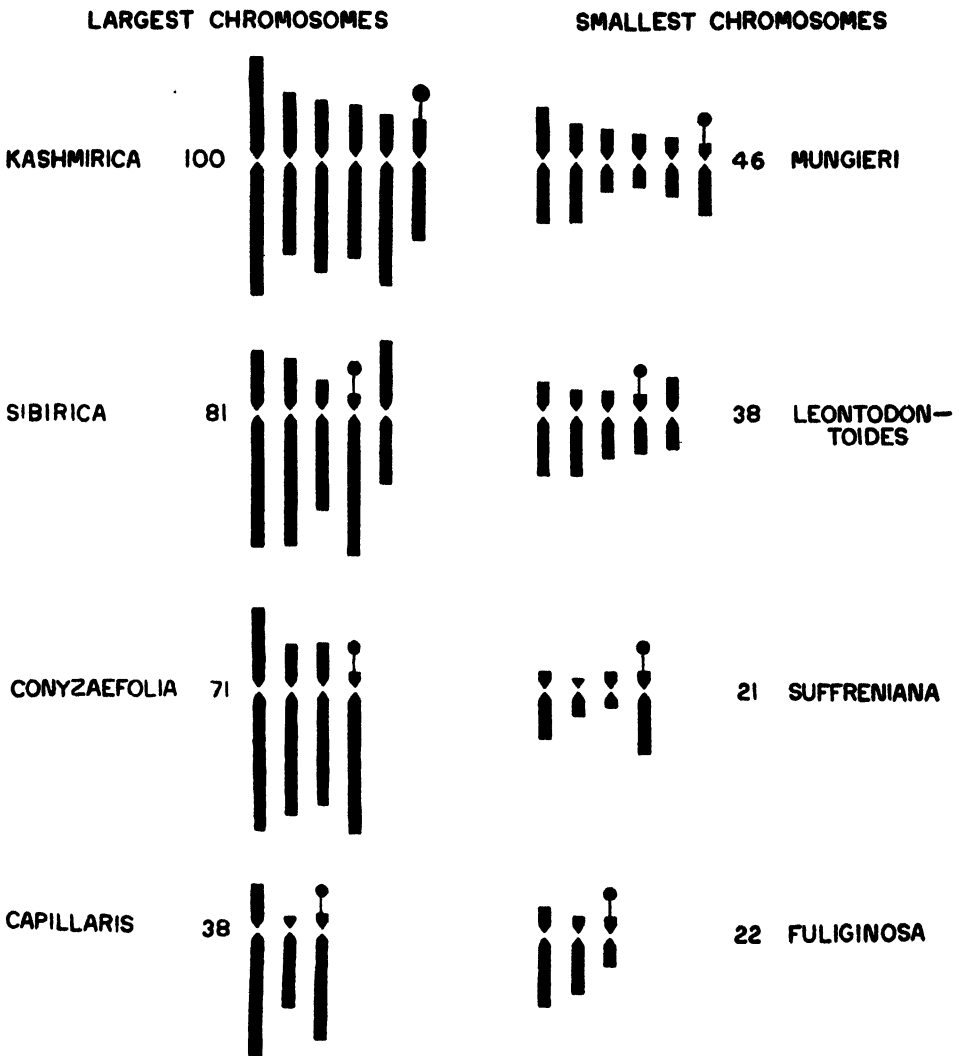


Fig. 2. Idiograms of the species with longest and shortest total chromosome length in each of the four number classes, $n = 6, 5, 4$, and 3. The reduction in symmetry is emphasized by placing the spindle-fiber constrictions on a common baseline in each number class. Using the total length of the somatic chromosomes in *C. kashmirica* as a base of 100, the proportional total length of each idiogram is shown by the number between the name of the species and its idiogram. With respect to the absolute size of the individual chromosomes, these idiograms are accurate only to a degree sufficient for purposes of the present discussion.

4) A decrease in chromosome size is the least well marked of the evolutionary trends. It is to a limited but not invariable extent correlated with a parallel decrease in total size of the plant. It is frequently associated with a specialized and restricted distribution of the species.

Babcock and Jenkins (1943), reporting on 113 species of *Crepis* representing twenty-three of the twenty-seven sections recognized in this monograph, reached the following conclusions:

1) The general trends of karyotype evolution in this genus are: (1) decrease in chromosome number; (2) increase in asymmetry of the chromosomes; and (3) decrease in chromosome size. These trends are all indicated by the idiograms of the eight species shown in figure 2 (see legend). These trends in karyotype evolution have occurred independently of processes resulting in morphological change.

2) Decrease in chromosome number has been progressive, from $n = 6$ to $n = 3$. The process went on step by step, through the loss of one chromosome at a time; and each step occurred independently on several different occasions. The evidence from *Crepis* supports Navashin's (1932b) dislocation hypothesis; that is, change in chromosome number through reciprocal translocations. In addition to the main trend of decrease in number, there have also been increases in number in certain restricted groups, such as amphidiploid hybrids and polyploids of various types.

3) Chromosome asymmetry is a further consequence of unequal reciprocal translocations; this, in spite of the fact that once the initial asymmetry is established the process does produce an opposite trend toward symmetry. In the long run the latter tendency predominates to a greater or less degree. Although it is impossible to recognize in *Crepis* a phylogenetic sequence on the basis of chromosome asymmetry, yet, in general, the more primitive species in the genus have more symmetrical chromosomes than the more advanced species (see fig. 2).

4) The decreasing trend in chromosome size also fails to follow a strict phylogenetic sequence. Although there is a general tendency for reduction in chromosome size, together with concurrent reduction or specialization of the plants and with a shortening of the length of the life cycle, yet, at the same time, there are numerous exceptions. The factors influencing this trend in *Crepis* are evidently complex, since they may reflect different physiological states which in turn may be influenced by various environmental factors. But it may be assumed that the physiological differences which characterize the species are gene determined; and therefore gene mutations may furnish the basis for the trend in decreasing chromosome size.

On account of the existing diversity in usage of the terms gene and gene mutation, it seems advisable, for sake of clarity, to define them here.

The term *gene*, as used in this monograph, means one of the hereditary units which make possible the particulate nature of inheritance, the phenomena of Mendelism and linkage. A more precise definition, in physical terms, need not be essayed here. It is well known, however, that the genes exist in the chromosomes; also that a chromosome includes a series of regions which are marked off by points or zones of potential breakage. Any such region makes up only a very small part of the length of a chromosome, is self-reproductive, and has a specific controlling action on cell physiology. The idea that each gene is a material entity of some sort and is situated in a particular gene region is a generally used concept.

Gene mutation means any change in a gene region which alters its action in cell physiology and is maintained in chromosome reproduction; it includes, therefore, those aspects of alterations in the linear order of gene regions known as position effects. Evidently such alterations also occur within gene regions (Goldschmidt, 1945, pp. 526-527). According to Huxley (1943, pp. 50-51), "a gene mutation will

then be any intrinsic change in substance or structure affecting the mode of action of one of these unit regions"; and "gene mutations (including position effects) appear to be the most important source of novelty in evolution. . . ."

GENETIC AND CYTOGENETIC RESEARCH, 1923-1942

It was from Dr. H. M. Hall that the author received the first suggestion regarding the application of genetical methods to the solution of taxonomic problems. At Hall's invitation the present author undertook genetic research on the common hayfield tarweeds of California which led to a joint publication (Babcock and Hall, 1924) in which the evidence from experimental genetics was combined with evidence from ecological and herbarium studies in working out a difficult problem in plant systematics. Along with the pioneer work of Dr. J. Clausen on *Viola* (1921-1922), these investigations comprise the earliest efforts known to the present author to synthesize the evidence from research on genetics, comparative morphology, and geographic distribution in attempting to discover a truly natural basis for the systematic treatment of a group of plants. Hall's point of view in this early work was essentially that of the "new systematics" of today, since he held that the taxonomist should think in terms of evolutionary processes and should learn to treat his morphologic criteria as dynamic rather than static. In short, it was Hall's emphasis on the phylogenetic viewpoint in taxonomy which led the present author to undertake, with the aid of various co-workers and students, the investigations on the genetics and cytogenetics of *Crepis* which have made possible the present attempt at a phylogenetic treatment of this genus. Since a complete historical record of all this research would require too much space and would be of doubtful value, the following topical treatment presents those results of the investigations which are of most significance for biosystematy.

The studies on the genetics of various species of *Crepis* have been summarized by Babcock and Navashin (1930, pp. 47-52) and Babcock (1942, pp. 161-162). The actual work was done by a number of different associates, the most important contributions being made by Collins (1924), Hollingshead (1930a), Babcock and Cave (1938), and Jenkins (1939). In general, the Mendelian inheritance of many morphological and of some physiological differences within species was clearly demonstrated; and quantitative differences were shown to be conditioned, as a rule, by multiple genes, although dwarf forms were discovered in certain species to be dependent on a single genic difference.

The first interspecific hybrids in *Crepis* were reported by Babcock and Collins (1920), but, during the following decade, the data on interspecific hybrids accumulated rapidly. The bearing of many of the findings on interspecific relationships was recognized as being so significant that it was decided to concentrate mainly on this phase of genetic and cytogenetic research rather than to attempt to make an extensive genic analysis of any one species. These investigations on interspecific hybrids have been reviewed in part by Babcock and Navashin (1930, pp. 37-43, 53-63) and by Babcock (1942, pp. 161-164, 173-178). The results also represent the efforts of a number of different workers, both at Berkeley, California, and at Moscow, Russia. Many discoveries of importance for the systematics of the genus were made during the course of these investigations. The following deserve to be mentioned because of their bearing on our phylogenetic and taxonomic concepts.

The simple genetic basis of receptacular paleae.—The discovery by Collins (1924) of a plant of *Crepis capillaris* with well-developed paleae on the receptacle and his demonstration that presence and absence of the paleae behave as a pair of Mendelian characters has an important bearing on the delimitation of the genus. The

small genera, *Pterotheca*, *Lagoseris*, and *Rodigia*, had been separated from *Crepis* primarily on the basis of presence of paleae on the receptacle. Now the question arose, since presence or absence of paleae within *C. capillaris* rests on such a simple genetic basis, is one justified in maintaining the three small genera just mentioned? Several years later Mrs. Cave (Babcock and Cave, 1938) found from crosses between *C. foetida commutata* (= *Rodigia commutata*), which has receptacular paleae, and *C. foetida vulgaris*, which has none, that presence and absence of the paleae are dependent on three genes, two primary and an inhibiting one. Thus, the one feature by which the former genus *Rodigia* was separated from *Crepis* was also shown to have a simple genetic basis. The hybrids between *R. commutata* and *C. foetida* were vigorous and highly fertile and they produced vigorous, fertile progeny. Furthermore, the geographic areas of the two entities overlap and intergrading variants occur. Hence, by this one experiment it was shown not only that *Rodigia* should be merged with *Crepis*, but also that the hybrid fertility relations are such that *R. commutata* must be reduced to the rank of subspecies. Finally, since occasional plants of *Crepis sancta* (= *Pterotheca sancta*) have been found which lack paleae on the receptacle, and since the plants are otherwise entirely *Crepis*-like, it has been assumed that both *Pterotheca* and *Lagoseris* should be merged with *Crepis*.

Interspecific lethal genes in Crepis.—An interspecific lethal factor was discovered by Hollingshead (1930a) in *Crepis tectorum*. It was found that some strains of this species, when crossed with *C. capillaris*, would produce only plants which died in the cotyledon stage, whereas others would give all viable offspring, and still others about half-and-half viable and inviable. Further tests proved that this factor behaved as a simple Mendelian recessive. Since normal meiosis in *C. tectorum* is always regular, it may be assumed that this factor is not a structural difference in the chromosomes of the different races of *C. tectorum*, but simply a gene. It was also found by Hollingshead (1930a) that, in crosses between *C. tectorum* and *C. bursifolia* and between *C. tectorum* and *C. leontodontoides*, both viable and inviable progeny occur in the proportions expected if the *C. tectorum* lethal were effective. But her data on *C. tectorum* × *C. vesicaria taraxacifolia* and on *C. tectorum* × *C. setosa* indicate that the lethal gene is ineffective in these hybrids. Certain other data on interspecific crosses not involving *C. tectorum* indicate that similar lethals may exist in other species of *Crepis* not yet subjected to genetic investigation. It should be noted that some of the strains of *C. tectorum* used by Hollingshead were of wild origin and from widely separated localities. Evidently this lethal originated either long ago or more than once in the history of this species. Since the closest relatives of *C. tectorum* are *C. Bungei* and *C. ircutensis*, it would be of interest to investigate the behavior of hybrids between these three species. If the lethal gene proved to be effective in hybrids between *C. tectorum* and the other two, the probability of its importance in the evolution of *C. tectorum*, which is the most advanced of the three species, would be greatly strengthened. Only three other cases of interspecific lethals or semilethals have been reported. One is in cotton (Hutchinson, 1932; Silow, 1941), and two are in *Drosophila* (Crow, 1942; Patterson, 1944). The evolutionary significance of the four cases is discussed by Patterson (*op. cit.*, pp. 219–220).

Crossability, hybrid fertility, and taxonomic relationship.—We are here concerned with the correlation between the genetical evidence and the degree of taxonomic relationship of the species as determined from comparative morphology. Interspecific hybridization has been conducted on an extensive scale in *Crepis*. The compatibilities of 35 species between which hybrids were obtained before 1930, as indicated by seed production under open-pollination, were reported by Babcock

and Navashin (1930). Between 1920 and 1939 data were obtained on about 200 interspecific hybridizations involving 55 species. The data on crossability, viability, and fertility are presented in chapter 3 (pp. 58–61). In general, as would be expected, hybrids between species which are less closely related, as judged from morphology, tend to be weak and sterile or, if vigorous, to be sterile or of very low fertility; whereas hybrids between more closely related species tend to be vigorous and more or less fertile. The evidence obtained from interspecific hybrids in *Crepis* and its bearing on taxonomic concepts are summarized in chapter 3 (pp. 52–58). Negative evidence on crossability may be of slight significance, but positive evidence in the form of hybrids, together with data on their fertility, is a valuable criterion of relationship. Much remains to be done to amplify the evidence on crossability and hybrid fertility. Of considerable significance is a hybrid between *Crepis sancta* of section 22, *Pterotheca*, and *C. leontodontoides* of section 14, *Mesophyllion*, growing in our greenhouse now (June, 1943). The latter species has been especially useful in obtaining interspecific hybrids. Several earlier efforts to make this cross had failed; but now a vigorous hybrid plant provides additional evidence of the close genetic relationship of *Pterotheca* and another section of *Crepis*.

Chromosome pairing in species and hybrids.—The diploid species of *Crepis* in general are highly regular in the behavior of their chromosomes during meiosis. Perfect pairing of the chromosomes was observed in *C. aspera* and *C. bursifolia* by Clausen (Babcock and Clausen, 1929). Complete or nearly complete regularity was reported in *C. tectorum* by Hollingshead (1930b); in *C. syriaca* by Cameron (1934); in *C. foetida* and *C. eritreënsis* by Babcock and Cave (1938); in *C. divaricata*, *C. Noronhaea*, *C. canariensis*, and *C. vesicaria* by Jenkins (1939); and in the sexual, diploid forms of *C. acuminata* and *C. occidentalis* by Stebbins and Jenkins (1939). Frequent failure to conjugate on the part of the members of one of the 5 pairs of chromosomes in a certain strain of *C. foetida rhoeadifolia* was explained by Poole (1931) as probably due to a constantly observable difference in size of the satellite borne by the members of this pair. In a certain strain of *C. capillaris*, known as the "X-strain," Hollingshead (1930b) observed univalent chromosomes at metaphase in from 12 to 44 per cent of the pollen mother cells of different plants growing under the same favorable conditions. It was discovered by Richardson (1935) that the occurrence of univalents at first metaphase in this strain is caused by failure of chiasma formation between homologous chromosomes which were found to be regularly associated in earlier (pachytene-diakinesis) stages. This, however, is exceptional, for such marked variations in metaphase pairing is not generally characteristic of diploid species.

The evidence on chromosome pairing in the first meiotic division in pollen mother cells of eleven interspecific *Crepis* hybrids was reviewed by Babcock and Emsweller (1936). Comparison of the average amounts of pairing at first metaphase in these hybrids leads to the conclusion that the genic complements of the fourteen species involved are all more or less homologous. This inference is consistent with the evidence on chromosome morphology in the genus, on geographic distribution, and on the results of the research on small groups of closely related species discussed above. This evidence on metaphase pairing in interspecific hybrids, therefore, supports the conception that the species of *Crepis* had a common origin and are still more or less similar in genetic constitution. At the same time it should be noted that more recent and detailed research on certain other interspecific *Crepis* hybrids has shown that meiotic irregularities in these hybrids are caused by differences in the structural arrangements of certain segments in the chromosomes of the parental species (see below, under the role of structural rearrangements in differentiation).

Polyploidy, autopolyploidy, and new species.—Although polyploidy is not of major importance in the genus as a whole, yet it does exist in certain species of *Crepis* and, in fact, has played an important role in the evolution of most of the American species (see below). One of the few Old World polyploid species is the widespread *C. biennis*, which was among those acquired early in the history of these investigations. *C. biennis* usually has 40 chromosomes in its somatic cells. When it was crossed with *C. setosa*, which has 8 chromosomes, the F_1 hybrids were found by Collins and Mann (1923) to have, as expected, 24 chromosomes. But, at metaphase in the pollen mother cells of these hybrids, they observed 10 pairs and 4 single chromosomes; and further investigation proved that the 10 pairs were formed by the 20 from *C. biennis* and the 4 singles were those contributed to the hybrid by *C. setosa*. This automatic pairing of the chromosomes of *C. biennis* among themselves in the hybrid was a most striking example of autopolyploidy, a phenomenon discovered by Rosenberg (1909b) in *Drosera*. All of the evidence from this hybrid and its derivatives indicates that *C. biennis* is an octoploid species with the base number $x = 5$, a conclusion of importance in establishing the phyletic relations of *C. biennis*. As a result of autopolyploidy among the *C. biennis* chromosomes and random distribution of the *C. setosa* chromosomes, the gametes of the F_1 hybrids received 10 *biennis* + 0 to 4 *setosa* chromosomes. Among the selfed progeny of such a hybrid there was one plant with 24 chromosomes which proved to be 10 pairs from *C. biennis* and 2 pairs from *C. setosa*. This new type combined characteristics from both parent species, and the first few generations obtained from the original plant were fairly uniform. Accordingly, it was named *C. artificialis* (Collins, Hollingshead, and Avery, 1929). In later generations, however, considerable variation in chromosome numbers was found among the progenies of selfed plants; and, as a result of testing selected individuals, Jenkins (unpublished) has obtained strains with various diploid numbers ranging from 20 to 36. Some of these strains appear to be fairly uniform morphologically, and it is possible that they might become established as natural species if given an opportunity in the wild. Although these investigations have revealed one process by which new species may originate in nature, yet there is no evidence that any existing *Crepis* species did originate from hybrids between species with such widely different chromosome numbers as those of *C. biennis* and *C. setosa*. However, a somewhat similar process involving interspecific hybridization seems to have been of great importance in the origin of several American species of *Crepis* (see below).

The evolutionary role of gene mutations.—Gene mutations, such as those causing naked receptacles and interspecific lethals, are doubtless of importance in the evolution of *Crepis*; but it is the great mass of less obvious mutations, causing small changes but affecting any part of the plant, which provides most of the material for intraspecific differentiation. The evidence from *Crepis* certainly indicates that, given some kind of isolation (cf. pp. 147–151), intraspecific differentiation leads eventually to the origin of new species. Many species of *Crepis* are polymorphic and twenty species consist of more or less well-defined geographic races or subspecies. In several of these which have been investigated cytogenetically the chromosomes of the subspecies appear to be identical and evidently differ from one another only with respect to certain genes. Such species are probably in process of differentiation as a result of mutation accompanied by selection under varying environmental conditions. Excellent examples are *C. foetida* and *C. vesicaria*, each of which is actually a superspecies composed of several distinct but interfertile subspecies; each of these subspecies has a wide distribution, but sufficient overlapping allows swarms of intergrading hybrids to occur. One can imagine what would happen if some sort of barrier, such as intersterility, were to separate

one of the subspecies from those with which it comes in contact. Its status would change to that of species in course of time, if not rapidly. This is actually what has happened in two groups of very closely related and rather thoroughly investigated *Crepis* species; but, here, the isolating barrier is geographic instead of genetic.

Crepis foetida and two close relatives.—In addition to *C. foetida*, Babcock and Cave (1938) studied *C. eritreënsis* and *C. Thomsonii*. From their geographic distributions (fig. 203), it is clear that the two latter species are widely separated from each other and from *C. foetida*. *C. Thomsonii* and *C. foetida* have closely similar karyotypes, and the chromosomes of *C. eritreënsis* exhibit only small differences from those of the other two species. In F_1 hybrids between any two of these species the pairing of the chromosomes in meiosis is practically perfect, indicating no large structural differences between the species. However, a comparison of meiosis in F_1 hybrids between each of these species and one 4-paired species (Sherman, 1946) indicates the existence of some structural differences in the chromosomes of these three species. Morphologically, the plants are sufficiently similar to be placed in the same subgroup of the same section; yet the genetic evidence shows that they differ in numerous genes. The fertility of the F_1 hybrids varies from very high in some to very low in others. It is sufficient, however, so that if the geographic ranges could overlap, the species would probably become merged and then *C. eritreënsis* and *C. Thomsonii* would have to be treated as subspecies. But these species do not approach one another closely at present, and there is no reason to anticipate that they will meet for an indefinite period of time. To this fact may be added the following reasons for considering *C. eritreënsis* and *C. Thomsonii* to be species: (1) they differ from *C. foetida* in many, not few, genes; (2) F_2 data from crosses show that these two species differ more from *C. foetida* in respect to self- and cross-compatibility than the various strains of *C. foetida* differ among themselves; (3) they both differ from *C. foetida* in the genes conditioning color of the ligules and the presence of red ligule teeth; (4) *C. eritreënsis* has monomorphic achenes, while *C. Thomsonii* and *C. foetida* have dimorphic achenes; (5) both species differ from *C. foetida* and from each other in certain other morphological features and both have a shorter life cycle than the most precocious form of *C. foetida*; and (6) both species show more morphological and physiological resemblance to *C. foetida vulgaris* than to the other two subspecies of *C. foetida*, even though the former subspecies is farther removed from them geographically. This indicates a phylogenetic connection fairly remote in time. During an ensuing epoch, barring a catastrophe and assuming continuation of the present balance between evolutionary pressures, these species may become much more distinct from *C. foetida* than they are at present through the accumulation of gene mutations.

Four insular endemics.—The other group of closely related species was investigated by Jenkins (1939). The group consists of four species: *C. canariensis* of Lanzarote and Fuerte Ventura of the Canary Islands; *C. divaricata* of Madeira; *C. Noronhaea* of Porto Santo Island near Madeira; and *C. vesicaria andryaloides* also of Madeira but well isolated from *C. divaricata*. *C. vesicaria andryaloides* is treated as a subspecies because *C. vesicaria taraxacifolia* has been introduced into Madeira, because it has invaded the area occupied by subsp. *andryaloides*, and because the two have become merged in a hybrid swarm. The facts about these five entities, with respect to morphological similarities and differences, chromosome similarity and meiotic regularity in parents and hybrids, and the genetics of quantitative and qualitative differences, are practically identical with those concerning the three species considered above. Among the five entities, Jenkins found a great many morphological differences affecting all parts of the plant. In his experimental

F₁ hybrids he found the average fertility, as indicated by percentage of seed setting in the open, was 25 to 50 per cent. The least fertile hybrids had only 1 to 2 per cent, and the most fertile 50 to 75 per cent, as compared with nearly 100 per cent in all of the parents. Thus, interfertility between all four species has been definitely though not completely reduced. The available cytological evidence certainly indicates that the five entities have a similar arrangement of genes in each of their 4 chromosomes. The cytological evidence, however, does not include detailed pachytene studies, and it is quite possible that minute structural differences are also present in these species. The situation is comparable to that reported by Silow (1944) for *Gossypium arboreum* and *G. herbaceum* in which "there is on the whole so extremely little cytological irregularity between the species that their differences must be referred, in the main, to a genetic basis." Therefore, the varying degrees of genetic isolation which have already developed in these species must be largely, if not wholly, the result of gene mutations.

Other evidence.—Babcock and Navashin (1930) report the result of crossing two diverse forms of *C. capillaris*, a low diffuse plant found in the Pyrenees, and a robust variant from northern Europe. The F₁ was intermediate in size and habit and was not over 50 per cent fertile. Also, in *C. tectorum*, a cross between a Scandinavian dwarf variant (var. *pygmaea*) and a tall form from Russia gave an intermediate F₁ with 50 to 60 per cent estimated fertility. Meiosis not having been studied in these hybrids, the evidence is incomplete. But, with more extensive research on intra-specific hybrids, probably many more cases of partial sterility between subspecific entities having no detectable structural differences in their chromosomes would come to light. From the evidence submitted, it is clear that in *Crepis*, at least, gene mutations comprise a genetic process of major importance in interspecific differentiation. In addition to their function in building up intra- and interspecific sterility, they are omnipresent and may at any time operate to supplement and extend the other genetic processes concerned in the evolution of species.

Experimental induction of mutations.—The experimental work on the induction of mutations in *Crepis* has been directed mainly toward the production of structural changes in chromosomes; but, in connection with some of this work, new gene mutations have been noted. Two general methods have been used, namely, the application of x-rays and the aging of seeds. All of the published research on *Crepis* in this field has been done by Russian botanists.

Effects of x-rays and neutrons on the chromosomes.—Navashin (1931a, b, c) initiated experimentation with the effects of x-rays on *Crepis*, using *C. tectorum*. Various categories of chromosomal alterations were observed, including translocations between nonhomologous chromosomes, which are the most important type of structural change in the evolution of *Crepis*. Levitsky and several associates (1931–1934), reporting experiments with *C. capillaris*, assumed that all the translocations observed were nonreciprocal. But, later, Levitsky (1935) concluded that the translocations he observed in *C. capillaris* were mostly, if not all, reciprocal. From the analysis of somatic plates in which the "shortening curves," representing changes in the longer arm of all three chromosomes, are compared, he concluded that breaks leading to reciprocal translocations occur shortly before the metaphase stage of cytokinesis. Korjukaev (1940) corroborated Levitsky's conclusion that the translocations induced by x-rays in *C. capillaris* are reciprocal. Levitsky (1937, 1940) also reported numerous other observations on chromosome alterations induced by x-rays, but these need not be discussed here. Kostoff (1943) reports that treating seeds of *C. capillaris* with a total neutron dose of about 20,000 r caused changes in the karyotype in 70 per cent of the cells examined. Most of the dislocations consisted

of fragmentations and translocations, and all 3 chromosomes were involved. Evidence of inversions was also observed.

Effects of the aging of seeds.—The aging of seeds as a cause of chromosomal mutations was first reported by Navashin (1933b), who states that seeds of *C. tectorum* show only 2 to 3 per cent germination when kept six to seven years. Chromosomal translocations were found in 81 per cent of the seedlings. He also reported (1933c) that the process of mutation in resting seeds was accelerated by increased temperature. Shkvarnikov and Navashin (1934) reported that fresh seeds of *C. tectorum*, after exposure to a temperature of 54 to 55° C for twenty, forty, and forty-four days, showed chromosome abnormalities, just as they did when exposed to increasing doses of x-rays. Of 106 roots of surviving plants (from twenty days' exposure), 14 showed chromosome translocations. Navashin and Gerassimova (1935, 1936) reported important additional observations on the chromosomal alterations occurring in the resting embryos of seeds. The evidence does not prove that all the translocations are reciprocal, but this is very probable. Certain of their data furnish good support for the "dislocation hypothesis" of evolution of basic chromosome numbers (see below). Translocations and inversions also probably play an important role in evolution as factors causing physiological isolation (cf. Gerassimova, 1935; Dobzhansky, 1941). Shkvarnikov (1939) reported that temperature, humidity, and other factors cause mutations in stored seeds through the physical and chemical processes taking place in the seeds; and similarly with mature pollen. Mutations of various sorts were observed, including both chromosomal and "point" or gene mutations. He inferred that in nature such variations must occur with high frequency when favorable conditions exist.

Most recently, Navashin, Gerassimova, and Belajeva (1940) analyzed the results of storing seeds of *C. capillaris* and *C. tectorum* for two, three, four, and five years in a basement where temperature and humidity fluctuations were recorded. A striking difference in the two species was observed in the effects of storage on germinating power and viability of the seedlings. As had been observed in earlier work, the seeds of *C. capillaris* showed much greater resistance to the effects of storage. This difference between the two species, it was pointed out, indicates an important adaptation in *C. tectorum*. Whereas *C. capillaris* is a typical annual, and its seeds normally germinate in the spring after 250 to 270 days of dormancy, *C. tectorum* is a "winter plant," that is, its seeds germinate soon after maturation and the vegetative rosettes live through the winter, the plants flowering the following season. (It should be noted that this physiological peculiarity of *C. tectorum* has been of value to the present author as an aid in determining the interspecific relationships of this species.) Since *C. capillaris* was found to be a favorable species, a thorough investigation was made of the occurrence of structural chromosomal mutations in increasing storage periods. In brief, it was found that the percentage of such mutations increased very rapidly after a certain period of time, whereas the percentage of mortality of embryos and seedlings increased uniformly throughout the entire period of storage. From this, it was concluded that an actual biological process was involved in the rapid increase in percentage of mutations; and it was inferred that increased humidity was the determining factor causing the increase in mutations. This led to the suggestion that seeds stored naturally in any place where the temperature was lower and the humidity higher than on the surface of the soil might contain a greater proportion of mutations.

Spontaneous mutations.—Spontaneous structural chromosomal alterations were reported by Navashin (1931c, 1932a, 1933a) in *Crepis*. The significance of such spontaneous mutations was emphasized by him (1931c) as follows: "It is obvious

that any heterozygous dislocation (translocation) would ultimately result in gain or loss of chromatin material in succeeding generations owing to segregation of chromosomes. And, if not incompatible with life, these may result in variations of evolutionary significance. For there can be hardly any doubt that the evolution of *Crepis* species was primarily based upon changes in the quantity of material contained in the individual chromosomes."

The evolutionary role of large changes in chromosome structure.—Structural changes in the chromosomes, leading to chromosomal transformation, alteration of karyotypes, and changes in chromosome number, have long been recognized as of fundamental importance in the evolution of *Crepis* (Hollingshead and Babcock, 1930). In the light of accumulated evidence, the conclusion that this process has been of primary importance in *Crepis*, and probably in several other genera, appears to be warranted. The hypothesis of Delaunay (1926) that reduction in *absolute size* of the chromosomes often accompanies evolutionary advancement is in general agreement with the evidence on phylogeny, as based on comparative morphology of the plants and chromosome size, not only in *Crepis*, but also in *Lactuca*, *Prenanthes*, and *Ixeris* (Babcock, Stebbins, and Jenkins, 1937), even though there are certain exceptions to the general rule. The hypothesis of Levitsky (1931) that primitive species have more numerous chromosomes with *median constrictions*, with the chromosomes comprising the karyotype nearly equal in size, and that, *along with advancing evolution, subterminal constrictions are developed* and the chromosomes become fewer in number and more unequal in size, is supported by the evidence from *Crepis* and from related genera (Babcock, Stebbins, and Jenkins, 1937).

Navashin's dislocation hypothesis.—From her evidence on partial metaphase pairing in hybrids between *Crepis* species with different chromosome numbers and different karyotypes, Avery (1930) inferred that the chromosomes of the different species contained some genically homologous segments. She suggested a scheme of karyotype transformation, involving reduction in number from 5 to 4, based on several types of structural change. Such evidence, together with the appearance of new types of chromosomes in the progenies of two triploid hybrids in *Crepis*, led Navashin (1932*b*) to propose his "dislocation hypothesis," which he based on the following facts: (1) chromosome number is conditioned by the number of centromeres which cannot be formed *de novo*; (2) segments of chromosomes may be lost or transferred to other chromosomes and this "dislocation" process may occur in both somatic and germ cells; and (3) the normal effect of a given portion of chromatin does not depend on the particular place it occupies in the chromosome system; and regular pairing in meiosis does not depend on the similarity of whole chromosomes, but on similarity of elements occupying corresponding levels in the conjugants. Hence, *the only conceivable way of changing the chromosome number is by addition or loss of one or more centromeres combined with appropriate dislocation*. Changes in either the plus direction or the minus direction could be explained on this basis. Although the "dislocation hypothesis" assumed nonreciprocal translocations and dealt only with chromosome number as a specific characteristic, yet it did explain changes in symmetry of individual chromosomes and in the relative size of different members in a set. But it leaves unexplained the evolutionary transformations in absolute size and bulk of the chromosomes.

Evidence from structural hybridity.—Evidence showing that structural changes have occurred during the evolution of *Crepis* has continued to accumulate. The most convincing of such evidence has come from the analysis of meiotic irregularities found in interspecific hybrids. Müntzing (1934) studied meiosis in a hybrid between *C. divaricata* and *C. Dioscoridis*, each of which species has $n = 4$ chromosomes,

though they belong to different sections (23 and 25). In addition to an average of only 1.8 bivalents at first metaphase in the pollen mother cells, fragments were observed at diakinesis and metaphase, and in some first anaphase figures there were chromosome bridges and fragments, representing double attachment chromosomes. Müntzing concluded that the chromosomes of the two species have homologous segments and that a somewhat different position of these segments in the pairing chromosomes would, by crossing over, cause the bridges and fragments. Various alternative arrangements of the homologous segments could produce bridges and fragments, and fragments might also arise from association of nonhomologous segments at pachytene. These observations demonstrated a mechanism capable of giving rise to chromosomal alterations of evolutionary value.

Two similar investigations on interspecific *Crepis* hybrids have recently been completed. Sherman (1946) studied meiosis in the F_1 hybrids between *C. Kotschyana*, with $n = 4$ chromosomes, and six other species in the same section, 20, all with $n = 5$. Like most other 4-paired species, *C. Kotschyana* lacks the small V-shaped E chromosome which is present in its 5-paired close relatives (figs. 204–214). In all the hybrids chromatin bridges and fragments, similar to those reported by Müntzing, have been found; thus, the existence in the chromosomes of *C. Kotschyana* of certain segments which are homologous with segments in the chromosomes of its 5-paired relatives has been demonstrated. This evidence in itself is a strong indication that the 4-paired *C. Kotschyana* was actually derived from some 5-paired ancestor or ancestors, presumably by a process involving reciprocal translocation. The probable validity of this assumption is greatly enhanced by the results of the following investigation.

Tobgy (1943) studied *Crepis neglecta*, $n = 4$, *C. fuliginosa*, $n = 3$, both F_1 and F_2 hybrids, and certain hybrid forms found in nature. A study of meiosis in F_1 hybrids revealed definite evidence of the existence of homologous segments in the chromosomes of the two species. The A and D chromosomes of *C. neglecta*, through unequal translocation, gave rise to the A and D chromosomes of *C. fuliginosa*; and the B and C chromosomes of *C. neglecta*, through a similar interchange of segments, gave rise to the B chromosome of *C. fuliginosa*. One arm of the C chromosome of *C. neglecta* and its centromere are absent from the complement of *C. fuliginosa*. Hence, it may be inferred that the 3-paired *C. fuliginosa* has been derived from *C. neglecta*, or from a common 4-paired but now extinct ancestor, through a process involving chromosome interchange and resulting in reduction from 4 to 3 pairs of chromosomes, as well as in marked change in karyotype (see p. 9 and fig. 1). Although it must be admitted that the above conclusion is based on indirect evidence, yet this evidence is wholly consistent with the evidence from comparative morphology (see Part II, figs. 255, 257), from the hybrid progeny obtained (see p. 26), and from the geographic distribution of the two species (see Part II, fig. 241).

Since the meiotic irregularities observed in the hybrids discussed above are caused by differences in location of homologous segments in the chromosomes as they existed in the species before they were crossed, the question arises, how did these structural differences in the parental species originate? A general answer to this question is found in the results of the experiments on induced structural changes and on the occurrence of structural changes in the embryos of seeds stored under conditions of high humidity and high temperature. But the question still remains whether structural chromosomal changes *within a species* may give rise to *intra-specific sterility* sufficiently great to permit the accumulation of genic differences between the physiologically isolated races. In other words, do structural chromosomal changes provide a mechanism of intraspecific differentiation?

Gerassimova's achievement.—Karyotypically distinct new forms of *Crepis tectorum*, produced by treating pollen and moist seeds with x-rays, have been investigated by Gerassimova (1939). The main steps in the process of producing these new forms, necessarily omitting many details, are as follows: Two different reciprocal translocations were found among the progeny from x-rayed material. One involved the A and D chromosomes, and the other, the B and C chromosomes. When a strain homozygous for each of the two reciprocal translocations was established, it was found that they were morphologically identical with normal *C. tectorum* and just as self- and cross-fertile. Crossing these two homozygous strains produced F_1 hybrids in which each of the 4 chromosome pairs differed structurally; but the plants resembled normal *C. tectorum* except for their lower fertility. Among the progeny obtained by selfing these hybrids, one, called *C. Nova I*, was homozygous for translocations in all 4 chromosome pairs. In the next generation a plant was found that was homozygous for strikingly different translocations in all 4 pairs; it was called *C. Nova II*. Both of these karyotypically new strains were morphologically identical with normal *C. tectorum* and equally viable and fertile. But, when *C. Nova I* was crossed with normal *C. tectorum*, the F_1 hybrids were only 30 per cent fertile when self-pollinated and slightly more when open-pollinated.

Whatever the precise nature of the sterility of these hybrids may be, there has been created here a highly efficient genetic mechanism, causing isolation between two constant forms of the same species. It is also very probable that crossing over between homologous segments will produce further structural changes causing further sterility. According to Gerassimova, "It becomes inevitable, therefore, that the progeny of the hybrids in question contains a very limited proportion of individuals with intermediate characters, but consists of the two parental types and of individuals which repeat the original hybrid. In other words, there exists a situation characteristic of a hybrid between two genuine species." *C. Nova I* and *C. Nova II* are morphologically indistinguishable from the original *C. tectorum*; but "accumulation of mutational changes should undoubtedly lead in future to such distinction." Although not suggested by Gerassimova, it should be recognized that many or perhaps most of these new mutations, leading to morphological and physiological differentiation, would probably be gene mutations. Furthermore, that sterility of a more complex nature would be built up, along with morphological divergence, by ensuing gene mutations is clearly indicated by the partial intersterility which was shown by Jenkins (1939) to exist between species which differ only in Mendelian variations.

It has now been fully demonstrated that chromosome transformations, similar to those induced by Gerassimova in *C. tectorum*, are produced in considerable numbers in normal dormant seeds when stored under conditions of high humidity and high temperature. They also occur "spontaneously," though more rarely, in seeds stored under ordinary conditions. When one considers the endless variety of conditions under which seeds in nature may await a suitable opportunity for germination, it seems probable that here is an important natural source of this category of genetic evolutionary processes in plants, namely, structural changes in the chromosomes.

THE AMERICAN SPECIES

With the exception of *Crepis nana* and *C. elegans*, which have $n = 7$ chromosomes and belong in section 12, the other members of which are all restricted to Central Asia, all of the native American *Crepis* have the base number, $x = 11$. It was proposed by Babcock and Navashin (1930) and Hollingshead and Babcock (1930) that this group arose as amphidiploid hybrids between Asiatic or extinct American

species with lower chromosome numbers, probably $n = 4$ and 7 . This hypothesis has been greatly strengthened by the monographic work of Babcock and Stebbins (1938) and Stebbins and Babcock (1939), supplemented by the research of Stebbins and Jenkins (1939).

Of the ten species recognized, one, *C. runcinata*, has no evident connection with the other nine. This species consists of seven subspecies, all with the same chromosome number ($2n = 22$). It occurs widely in the western United States, the center of its distribution being the central Rocky Mountains. It is definitely mesophytic in its associations; and it is the only American species showing any indications of relationship with the Asiatic species, *C. gymnopus* of Japan and *C. praemorsa* of Eurasia, both of section 13.

The other nine species include seven diploid forms also with the somatic chromosome number $2n = 22$. These diploids are entirely distinct from one another, but they are connected by a continuous, complex series of intergrading, polyploid forms which are partly or wholly apomictic and which have somatic chromosome numbers ranging from 33 to 88. The polyploids are of two sorts: A few are morphological autopolyploids identical with the diploids except for their *gigas* characteristics; but most of them are allopolyploids which combine the characteristics of two or more diploids. Each of these seven diploid forms is confined to a single whole or part of a climatic province; six occur in northeastern California and adjacent Oregon; and two occur in central Washington, one of which extends into southern British Columbia. The autopolyploids do not occur outside the province occupied by the corresponding diploid. The allopolyploids show by their distribution the combination through hybridization of the physiological characteristics that determine their distribution. The different forms have different soil preferences, so that their distribution is partly governed by the occurrence of different geological formations; and this is also true of many Old World species.

These species with $x = 11$ were probably not all derived from the same hybrid. Not only does *C. runcinata* stand apart from the other nine; but, among the latter, three distinct subgroups must be recognized (see Part II, p. 572). And even among these subgroups there are strong individual specific differences. In fact, the Asiatic species which show the strongest resemblances to these American species are found in six other sections (see p. 69). Thus, several different hybrids must have been involved in the origin of these species and, since no evidence exists that any of the hybrids ever reached North America, it is probable that they occurred in Asia. After the amphidiploids reached North America two processes began. First, they hybridized to produce more or less sterile progeny, and at the same time they may have produced autopolyploid offspring. Second, by means of chromosome doubling in the diploid ($2n = 22$) F_1 hybrids, or by hybridization of autopolyploids of two different species, or between the autopolyploid of one species and the diploid of another, the various intermediate allopolyploids were produced. The subsequent evolution of the species in this section has been determined by hybridization, polyploidy, and apomixis, coupled with the selective effects of the environment.

GENETIC EVOLUTIONARY PROCESSES IN CREPIS

The subject of genetic evolutionary processes in *Crepis* has been discussed at some length by Babcock (1942) and by Babcock, Stebbins, and Jenkins (1942). But it seems appropriate to conclude this review of the research on *Crepis* having a bearing on systematics with a brief summary of the conclusions reached concerning the genetic processes which have been responsible for evolution in this genus.

Primary changes.—The genetic processes primarily causing evolution in *Crepis*

are gene mutations (see p. 12) and structural changes in the chromosomes leading to intraspecific sterility and karyotype evolution.

Gene mutations.—Two different aspects of *Crepis* evolution are found to depend upon gene mutations, namely, morphological and physiological differentiation, and accumulation of intra- and interspecific sterility; a third, reduction in chromosome size, may also be attributed to gene mutations.

1) Differentiation.—There are numerous polymorphic species of *Crepis*, for example, *C. capillaris*, *C. tectorum*, *C. Dioscoridis*, and *C. foetida*, in which genetic experiments have shown that intraspecific variations, both morphological and physiological, are Mendelian in their inheritance. There are also groups of very close species with identical karyotypes between which numerous Mendelian differences exist, for example, the group of insular endemics investigated by Jenkins (1939) and *C. foetida* and its two close relatives, *C. eritreënsis* and *C. Thomsonii* (Babcock and Cave, 1938). There can be no doubt that gene mutations have made possible the gradual accumulation of differentiating Mendelian variations in such species. Furthermore, this process of gene mutation is always going on and is ready to play its part whenever circumstances favor differentiation and discontinuity. When intraspecific isolation is accomplished through changes in chromosome structure, gene mutations will continue the process of differentiation.

2) Accumulation of intersterility.—In addition to Jenkins' insular endemics discussed above (p. 17), other evidence from *Crepis* exists showing that gene mutations cause the accumulation of intersterility in isolated populations. In the *C. foetida* group mentioned above, some of the first hybrids studied were highly fertile, whereas others were more or less sterile. It is safe to assume, therefore, that the interfertility relations among the species of this group is comparable to that found in the insular endemics. Then, we also have the evidence from intraspecific hybrids in *C. capillaris* and *C. tectorum* mentioned above. Although evidence is lacking on the regularity of meiosis in these two hybrids, their lowered fertility is probably due mainly to genic differences between the crossed strains.

3) Reduction in chromosome size.—The parallelism between the general trend toward reduction in chromosome size and progressive reduction in the plants and the length of their life cycles throughout this genus was mentioned above (p. 12). This parallelism in evolutionary trends was first mentioned by Babcock and Cameron (1934), without assumptions being made regarding its possible cause. Although no direct evidence regarding the cause of chromosome shortening is yet available in *Crepis*, plenty of evidence shows that the morphological and physiological variations in the plants depend on genic differences. Nor does evidence exist that such structural changes in the chromosomes as reciprocal translocations cause any somatic changes. This was pointed out in Gerassimova's translocant strains of *C. tectorum* (p. 22). Hence, the progressive reduction in size and length of life cycle so prevalent in *Crepis* must be attributed to the accumulation of gene mutations. It would seem reasonable, therefore, to assume that this trend in reduction in chromosome size is also a visible effect of genotypic changes. The contention that loss of large segments of euchromatin is the cause of general reduction in chromosome size is, of course, not to be considered because of the known deleterious effects of such losses. The loss of segments of heterochromatin may, in some instances, have caused reduction in length. This certainly is true of *C. fuliginosa*. As stated above (p. 21), this is the species which lacks parts of the C chromosome of *C. neglecta*, including the centromere, which parts, Tobgy (1943) points out, are largely composed of heterochromatin. That this sort of change is the chief cause of chromosome shortening, however, seems unlikely. This problem is discussed

further by Babcock, Stebbins, and Jenkins (1942, pp. 358–359) and Babcock and Jenkins (1943, pp. 271–272). Although it is impossible as yet to determine the exact nature of the genetic control of chromosome size, nevertheless, the fact of some genetic control of chromosome size is clearly indicated. Furthermore, the progressive reduction in the chromosomes, which has accompanied reduction in size and life cycle of the plants, may well depend upon gene mutations.

Structural changes in the chromosomes.—Changes in chromosome structure have been shown by the evidence reviewed above to have played two different roles, namely, the genesis of interspecific sterility and progressive differentiation in the karyotype. The relative importance of these roles in the origin of species is clearly indicated by the evidence from *Crepis*.

1) Genesis of intersterility leading to speciation.—The origin of intersterility within a species through changes in chromosome structure was beautifully demonstrated by Miss Gerassimova (1939). On *a priori* grounds this is the only role played by changes in chromosome structure which could be of primary importance in speciation. And, since the origin of such sterility might either precede or follow extensive differentiation through the accumulation of gene mutations, the one process, as a cause of speciation, cannot be considered any more basic than the other. This conception is advanced, however, with the one reservation that there is evidence from *Crepis* indicating that certain genetic differences among the individuals of a species have a marked effect on the frequency of occurrence of chromosome changes caused by x-rays. Levitsky (1937) reported that the chromosomes in *C. capillaris* are very stable, but that among 295 plants grown from x-rayed seeds, there were 25 showing deviations in chromosome morphology. These were confined to 11 out of 28 families and just 2 of these families had 11 of the 25 cases. Hence, he concludes, there are genetic differences conditioning structural instability and these may be an important cause of karyotype evolution. If future investigations should prove the existence of genes which condition liability to the occurrence of structural changes, then, to this extent, gene mutations would have to be considered a more basic process than gross chromosomal changes. For the present, however, both gene mutations and structural changes leading to karyotype evolution must be recognized as of primary importance, at least in plants.

2) Karyotype evolution.—Karyotype evolution in *Crepis* is characterized by progressive reduction in chromosome number, increase in asymmetry of the individual chromosomes, and reduction in total length of the chromosomes. (1) That the parallelism between reduction in chromosome number and reduction and specialization in the plants is coincidental should be emphasized. Evidence has been presented showing that reduction in chromosome number has been made possible by changes in chromosome structure, principally by reciprocal translocations; whereas progressive reduction and specialization of the plants has depended entirely upon gene mutations. Gene mutations and reciprocal translocations between chromosomes proceed independently but apparently fortuitously in *Crepis*, except so far as the latter may depend upon the former. (2) The parallelism between increase in asymmetry of the individual chromosomes and progressive evolution of the species is likewise apparently fortuitous. Modification of the individual chromosomes, like reduction in chromosome number, depends on such changes in chromosome structure as reciprocal translocation; whereas morphological and physiological differentiation within and between species depends on gene mutations. (3) Reduction in chromosome size, on the other hand, and reduction in the plants can logically be referred to the effects of gene mutations. This particular parallelism appears not unlikely to rest upon a common cause for both categories of phenomena.

Secondary changes.—The genetic processes involved secondarily in the evolution of *Crepis* are interspecific hybridization, polyploidy, and apomixis.

Interspecific hybridization.—The roles of interspecific hybridization are: (1) the origin of a small number of new species; and (2) the augmentation of karyotype evolution.

1) Origin of new species.—Although the evidence is necessarily all indirect, it appears practically certain that the ten previously discussed American species of *Crepis*, with the base number $x = 11$, provide convincing evidence that interspecific hybridization has been primarily responsible for a small but very distinct group of species now situated on the extreme periphery of the range of the genus. The seven species in section 12, *Ixeridopsis* (see Part II, pp. 528–547), and the five species in section 18, *Pyrimachos* (see Part II, pp. 632–648), may have originated through hybridization between certain ancestral species of *Crepis* and either *Ixeris* or *Youngia*. If the assumption of hybrid origin is true of all of these three groups, this accounts for only 11 per cent of the species in the genus.

2) Augmentation of karyotype evolution.—In Tobgy's (1943) research on *C. fuliginosa* \times *C. neglecta*, one of the F_2 segregants was similar in morphology and karyotype to a certain plant grown from seeds collected in the wild by Miss S. P. Topali in northeastern Thessaly, where it is known that the two species have come into contact. This particular form is about 70 per cent fertile. Its karyotype appears like that of *C. neglecta*, but one or more chromosomes contain segments from *C. fuliginosa*, which explains the presence of certain characters from that species. The occurrence of a duplicate of this wild form among Tobgy's F_2 segregants provides a clue to one method of the origin of intergrades occurring in nature. It also indicates that interspecific hybridization may operate as a secondary process in the origin of species through interspecific translocations leading to entirely new types of plants with new types of chromosomes.

Polyploidy and apomixis.—As is shown by the fact that comparatively few species exhibit either polyploidy or apomixis, both these phenomena are of secondary importance in the evolution of *Crepis*.

1) Polyploidy.—Among the rare polyploids that have been discovered in this genus, four have been so little studied that their classification as auto- or allopolyploid is purely conjectural. These are *C. polytricha* (Part II, p. 266), *C. incana* (Part II, p. 480), *C. taygetica* (Part II, p. 482), and *C. ciliata* (Part II, p. 433). The last-named species is certainly an octoploid, and, like *C. biennis*, it may be a doubled-up amphidiploid which arose from hybridization between two 5-paired species. In the complex polymorphic species, *C. vesicaria*, three of the subspecies, namely, *typica*, *taraxacifolia*, and *myriocephala*, are mostly diploid, but natural tetraploid forms occur which from their morphology certainly appear to be autopolyploids. But subsp. *stellata* appears on the same grounds to be an amphidiploid (or rather a mixture of amphidiploid forms and variants derived from them) originating from a cross or crosses between two other subspecies. Another tetraploid species, *C. crocea* (first reported by Hollingshead and Babcock, 1930, as *C. Bungei*, no. 2174), appears to be an amphidiploid derived from a hybrid between *C. Bungei* and *C. oreades* (see Part II, p. 504). In all but two of the native American species of *Crepis*, as was explained above, polyploidy has played an important role in differentiation and extension of the ranges. A similar situation seems to exist in the group of five species comprising section 18, *Pyrimachos*, of southeastern Asia. But in these the evidence rests entirely on morphological evidence, especially of the pollen grains.

2) Apomixis.—In all but one (*C. runcinata*) of the American species with the base number $x = 11$, apomixis has operated, along with polyploidy, to cause still greater

differentiation within this group. But the various intergrading complexes are not equally likely to persist. In some of them the diploid ($2n = 22$) form is dominant and aggressive in most parts of its range; whereas in other complexes the diploid is restricted in distribution. The latter type of species is destined eventually to become extinct. The ultimate fate of an agamic complex, of which the sexual ancestors have become restricted or extinct, can be predicted; it will persist so long as conditions remain favorable, but it will be unable to meet new changes in the environment and, therefore, will in time become more and more restricted and will eventually die out. As Stebbins (1941) concludes, apomixis is not a major factor in evolution, however important it may be in increasing the polymorphism and geographic distribution of the genera in which it is found.

In this connection it should be pointed out that the review by Huxley (1943) of the monograph on the American species of *Crepis* (Babcock and Stebbins, 1938) gives an unfortunate impression concerning the *evolution of the genus as a whole*. The statement: "we are given a very interesting picture of the varying roles of selection, environment and polyploidy in a facultatively apomictic plant genus" certainly does convey the idea that apomictic reproduction is common throughout the genus, whereas just the opposite is true. Polyploidy and apomixis play a relatively unimportant part in the evolution of the genus as a whole, no matter how important they have been in the differentiation and ultimate fate of nine of the native American species. And the only other group of *Crepis* species in which polyploidy and apomixis appear to have been of much importance is the group of five species comprising the section *Pyrinachos* of southeastern Asia. It is only fair to add, however, that the general reviews of the evidence on *Crepis* as a whole (Babcock, 1942; Babcock, Stebbins, and Jenkins, 1942) probably were not available to Huxley before the publication of his important book.

Finally, it should be noted that, although most of the *Crepis* apomicts are of hybrid origin (allopolyploids), yet hybridization is probably an accompanying phenomenon rather than the cause of apomixis. The presence of predominantly apomictic reproduction, together with the occasional production of hybrid and segregating types by means of the sexual process, accounts very well for the variability of these species.

SUMMARY

Two decades of research by numerous persons on various species and hybrids of *Crepis* have produced results of considerable significance for the problems of systematics in this genus. These results may be summarized as follows:

- 1) Comparative morphology provides the primary basis for inter- and intra-generic classification in the *Crepidinae*. But in *Crepis*, at least, the evidence from comparative karyology, genetics, and cytogenetics has proved to be of the greatest value in determining phylogenetic relations and thus in approximating a truly natural classification. The morphological criteria of relationship are discussed in chapter 3.

- 2) Chromosome number and morphology are both important in relation to phylogeny in *Crepis*. Of the 113 species studied cytologically, 97 are characteristically diploid species (in a few of them tetraploid variants sometimes occur, but even in these species, most of the plants are diploid). The other 16 comprise 10 American and 6 Eurasian polyploids. Among the 80 or more species which have not been studied cytologically, only the 5 species comprising section 18 give a strong indication of being highly polyploid. Thus, in the evolution of the genus as a whole, polyploidy has been of relatively slight importance, and apomixis is of still less significance.

Of the 97 known diploid species, all but 3 have either 3, 4, 5, or 6 pairs of chromosomes. The other 3 have 7 pairs, but, as was explained (p. 5), these require a special hypothesis concerning their origin. On morphological grounds the most primitive species have 6 and 5 pairs of chromosomes, and the most advanced species, 4 and 3 pairs. Furthermore, a definite parallelism exists between karyotype evolution in *Crepis* and progressive morphological reduction and specialization in the plants. This parallelism between the chromosomes and the plant morphology provides an unusually strong basis for the phylogenetic relations shown by the sequence of the sections in Part II. See also chapter 4.

3) Cytogenetic research has still further strengthened the evidence on phylogenetic relations in this genus by demonstrating the method by which reduction in chromosome number takes place (cf. Tobgy, 1943, p. 107). Of less significance in phylogeny, but of equal importance in evolution, is the demonstration by Miss Gerassimova (p. 22) that structural changes in the chromosomes may initiate differentiation within a species by creating intrasterile groups within it. Another important contribution of cytogenetics is the aid it has given in working out the especially difficult complexes of intergrading forms, which comprise most of the American species of *Crepis*, and the aid it has given in the phylogenetic treatment of this group.

4) Genetic investigations have shown that a few gene mutations may be responsible for morphological differences—receptacular paleae, for instance, which were previously used by taxonomists in defining generic limits. It has also been shown that gene mutations may be responsible for the accumulation of interspecific sterility, so that geographically isolated entities which are now partly intersterile may be expected to become more so in course of time, a consideration to be given due weight in delimiting species. Finally, the data which have been accumulated on interspecific hybrids in *Crepis* have been found to agree very well with the sectional classification arrived at primarily on morphological grounds (see chapter 3).

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CHAPTER 2

TAXONOMIC CONCEPTS

INTRODUCTION

ONE OF THE chief aims of the present author has been to convince others of the fundamental importance of a truly scientific taxonomy, that is, a taxonomy which rests upon the broadest possible foundation of biological disciplines. For only in this way will taxonomy come to occupy the fundamental place which it deserves in the realm of natural science or become "the focal point of biology" (Turrill, 1942, p. 690), and only in this way will biology in general come to rest upon the surest foundation. It therefore becomes necessary for any biologist, who wishes to understand the relations of taxonomy to his own field of work, to consider along with the taxonomist the basic concepts used in present-day systematics.

Since the eighteenth century it has been generally recognized among systematists that the basic concepts with which they must deal are those of genus and species. But the question whether those two terms denote nothing more than concepts or whether the specific and generic names applied to plants and animals designate real entities in nature is one on which there still exists diversity of opinion (Anderson, 1940; Camp and Gilly, 1943).

It appears that this diversity of opinion regarding the reality or nonreality of clearly recognizable smaller and larger groups of organisms is largely due to the difficulties in clearly distinguishing between the actual groups. These obstacles arise, it must be admitted, because Nature finds plenty of ways by which to make difficult the clear and complete delimitation of such natural groups. Nevertheless, early man became aware of the existence of genera of animals and plants. That the recognition of genera has actually been going on since or before the dawn of history is interestingly shown in the following quotation from Bartlett (1940) :

Classical botany was folk science. It did not progress far beyond the gathering together of folk beliefs and practical information. Theophrastus dealt almost entirely with cultivated plants, and Dioscorides with medicinal ones, and each systematized the knowledge or belief of his time with regard to the particular plants that interested him. Although they had no Dioscorides to record it, the illiterate barbarians of northern Europe probably had a folk science and terminology nearly as extensive and useful as that of Greece or Italy. Contemporaneously, an equivalent folk science would have been in Egypt, in Ethiopia, in Palestine, in Persia, in Mesopotamia. There is, as a matter of fact, a modern interpretation of an old Babylonian herbal. China has its ancient knowledge of plants with a surviving literary record in a long series of printed pents'ao or herbals dating back at least to 1100, and based upon folk science hundreds or thousands of years older. China passed its learning on to Japan, where there was certainly already a native lore which was grafted upon the Chinese. India early had symptoms of native medicine and associated plant lore which have come down to the present time partly by way of literature and partly by way of tradition. Anyone who delves into the beliefs of the peoples of the East Indies cannot fail to be impressed by the voluminous lore of plants, comparable in extent and value to that of the classical Greeks or Romans, and maintained by a nomenclature quite as scientific as the best in European botany during the time preceding Linnaeus. The New World had developed its own plant lore, an extensive body indeed in ancient Mexico, with its associated system of plant names and plant classification. Wherever we look into the matter, whatever the people or the language, we find naming and classification of plants, and almost invariably a more or less well-defined idea of the genus, as the smallest group that almost everyone might be expected to have the name for in his vocabulary. It might or might not be subdivided into species.

The idea that the generic concept is a characteristic of folk science will be found carefully developed in E. L. Greene's *Landmarks of Botanical History*. I have carried the development somewhat farther, anxious to show that the generic idea is concerned in its beginnings with the psychology of language, that those beginnings are lost in pre-history, and that we can only recover some conception of them by the consideration and comparative study of the plant names of people everywhere.

Another important reason for persistence of the confusion of thought concerning the reality or nonreality of species and genera is the practice of pigeonholing. The inadequacies of equipment and personnel in museums and herbaria throughout the world may be partly responsible for this practice. But unfortunately what might be condoned as a temporary expedient in filing specimens seems to have profoundly affected the thinking of many biologists. For, along with this practice, two tendencies have developed on the part of taxonomists: Some err to an extreme in the "lumping" of both species and genera, whereas others go to an extreme in the "splitting" of those same groups into segregates. All too often this lumping or splitting of truly natural groups has been based on purely artificial criteria. What, then, shall be recognized as the soundest criteria for the recognition of genera and species? The answer has been given in unmistakable terms by Hall and Clements (1923, p. 6) in the following paragraph on *the nature of the genus*.

In the prevalent view the genus appears to be regarded merely as a concept, and it is often stated that it does not actually exist in nature. This is doubtless true for those who regard the genus merely as a pigeon-hole, chiefly convenient for the filing of new species. Such a view has its justification in the usual practice of making genera, and especially in the recent flood of generic segregation. It is not supported by the evidence drawn from the methods of evolution or the record of phylogeny. To the student of evolution, the genus represents a certain characteristic portion of the line or field of specialization, and its existence is as definite as that of the species which constitute it. It may be more difficult to recognize, but this is primarily the fault of outlook and method. In the absence of definite criteria, the chief difficulty centers about the rank and limits of genera. As a consequence of the unrestricted play of personal opinion, not infrequently aided by bias or carelessness, present-day taxonomy contains genera of every possible quality. Many of these disappear completely when the test of evolution is applied to them. Given the family, genus, and species as major units, these will regularly be differentiated into tribes, sections, and variads, respectively. This is a necessary corollary of the principle that the processes of evolution are constantly and universally at work. The basic laws of conservation of energy and material, division of labor, and increase of parental care lead inevitably to divergence, and hence to the splitting of the generic stock into sections, and of the specific stock into variads.

That man's awareness of *species* has been a fundamental factor in his evolution and survival is emphasized by Camp and Gilly (1943, pp. 380-381):

There are even some among us who have advocated that we discard the concept of species altogether. Therefore, the question which the systematist should seek first to answer is not: Upon what criteria should the concept of the species-unit be based? Rather, he must enquire: Does the species-unit deserve to be a fundamental philosophical concept? This, perhaps fortunately for his own peace of mind, has long ago been decided for him.

The concept of species or *kind*, as a unit, has become so firmly entrenched in the mind of man—so much a part of his awareness, so necessary to his basic philosophy—that it remains only for the systematist to interpret this unit and give to it (1) a circumscription which is not only biologically as sound as possible, but (2) which also is in accord with an effective system of nomenclature. Furthermore, the interpretation of these items must be balanced; there must be no undue emphasis of one above the other, otherwise a bifurcation of concept will result leading to chaos in systematics. These two criteria—practical expedience in the interpretation of biological phenomena, and the application of an effective system of nomenclature—are the elements from which the systematist must fashion his concept of species.

In summarizing this brief introduction two thoughts need to be emphasized. First, many specific and generic groups of plants and animals have been recognized by man since time immemorial. Since these groups are objective realities, it may be assumed that all organisms may be classified into truly natural groups, provided that adequate criteria can be found for such classification. This, of course, is where the trouble begins; but because an achievement is difficult is no excuse for failing to attempt it. Second, the only criteria which can safely be used in establishing a natural classification of individuals into species and of species into genera are those which represent or reflect the evolution of those species and genera.

THE GENUS CREPIS

A review of the taxonomic history of *Crepis* (see Part II) reveals a continual swinging to and fro between lumping and splitting. This was caused largely by the lack of any fundamental guiding principle as a basis for classification. When the problem was taken up by the present author there were many species masquerading under the name *Crepis* which belonged in other genera. In many it was not difficult to show good reasons for their exclusion. For example, there are several South American and Mexican species of *Hieracium* with attenuate achenes and white pappus which had been described as *Crepis*. But it was found that in their other characteristics they were more like *Hieracium*; and when some of them were examined cytologically (for example, *H. Fendleri* = *C. ambigua* A. Gray) it was found that they have 8 or 9 pairs of chromosomes, like those of other species of *Hieracium*. A similar situation holds with other species representing *Lactuca*, *Ixeris*, *Launaea*, *Aetheorrhiza*, *Tolpis*, *Taraxacum*, and *Troximon*, not to mention several genera characterized by plumose pappus.

After such delimitation there still remained three groups of species which had long been accepted in *Crepis* and which were morphologically closer to *Crepis* than the genera mentioned above. But the cytological evidence, so far as the chromosomes had been examined, indicated that they were distinct phylogenetic groups. The cytological evidence on these and other related genera in the Crepidinae was reported later by Babcock, Stebbins, and Jenkins (1937). It was at this time that Dr. G. L. Stebbins, Jr., became associated with the author and undertook a general survey of all the genera in the tribe Cichorieae, giving special attention to the subtribe Crepidinae.

As a result of this survey, decisions concerning the three difficult groups mentioned above could be reached with considerably more assurance. The most important of these, phylogenetically, is the genus *Dubyaea* DC. As reconstituted by Stebbins (1940), this includes *Crepis bhotanica* Hutchinson (= *C. Dubyaea* Marq. et Shaw), *C. (Paleya) oligocephala* Sch. Bip., and *C. tsarongensis* Anthony, along with several other species which were not previously assigned to *Crepis*. The 9 species comprising this genus are all endemic in the Sino-Himalayan region. They are believed to be the living representatives of a larger group of species from which many of the genera in the subtribe Crepidinae originated. In the present author's opinion this genus had its origin in north Central Asia or farther to the east in northern Asia. This matter is discussed more fully in chapters 5 and 6. Another group of species, with a distribution resembling that of *Dubyaea*, had been referred to in the literature as the Glomeratae and had been recognized as showing affinity with *Prenanthes*. In fact, they had all been originally published as either *Crepis* or *Prenanthes*. This group became a new genus, *Soroseris* (Stebbins, 1940). Meanwhile, the third and most troublesome group of species had been disposed of by reviving the genus *Youngia* DC. and referring to it 19 species which had been originally described as *Crepis* (cf. Babcock and Stebbins, 1937). The reasons for the separation of all these species from *Crepis* are fully explained in the references cited. After all this work of delimitation, the net result is the assemblage of the 196 species included in this monograph. It is the author's firm belief that, with the exception of two small sections (12 and 18), they comprise a monophyletic group. Furthermore, these two sections (12 and 18) should, on morphological grounds, be included, even though they may have originated through hybridization between primitive *Crepis* species and species which became the ancestors of groups now recognized as different genera.

THE KINDS OF SPECIES FOUND IN CREPIS

The species concept has been one of the most controversial subjects of biological literature since the time of Darwin. In the present brief discussion, reference is made to only two of the earlier contributions which influenced my own views of this problem. Early in the present century Poulton (1908, pp. 46-94) published his illuminating essay, "What Is a Species," in which he reviewed the ideas of many of the older naturalists and set up several criteria that might be used in formulating a species concept. Robson (1928) presented a well-rounded discussion of the subject, with emphasis on physiological differentiation, distribution, isolation, and on correlation and the origin of groups. With these contributions as a basis, the present author (1931) formulated the following ideas as essential for a working concept of species:

1) Common structural characteristics which unite certain individual organisms into one group, and a common genetic basis for the group represented by a specific chromosome complement.

2) Characteristic features which distinguish such entities from one another, one of these features frequently being the chromosome complement.

3) Relative stability combined with more or less variability within the group. This stability is made possible by a high degree of regularity in chromosome distribution from cell to cell and from parent to offspring, while inherited variations arise from occasional changes of one sort or another in the chromosomes.

4) Common descent of all individuals of the group from one or more preëxisting species is made possible by the known mechanism of heredity and genetic variation.

5) Syngamy or free intercrossing and high interfertility among the individuals of the group are just what would be expected in organisms in which almost all of the genes in all of the chromosomes are homologous.

6) Absence of free intercrossing and usually high, if not complete, sterility in hybrids between different species (with a few exceptions) are logical results of the accumulation of genic and larger chromosomal differences between diverging groups of individuals within a species.

7) The existence in many species of subspecific groups, occupying different but usually overlapping geographic areas. These subspecies differ more from one another in structure and interfertility or both than do the individuals composing each subspecies, but the subspecies are sometimes still connected with one another by intergrading forms. This is the necessary result of genetic variability within the species, plus the influence of environmental variability, isolation, and natural selection or random fixation. It is a stage in one process of species formation.

The necessity of including the seventh item arises from the fact that some species are polymorphic, while others are not. It is for just such reasons that, up to the present, no fully adequate and satisfactory definition of the term species has been forthcoming (Mayr, 1942, p. 147). Although Hogben's assertion that "The word 'species' has no single meaning" (Hogben, in Huxley, 1940) is true; yet a concept of species sufficiently clear and definite for purposes of the present discussion can be stated briefly. Several such statements have been published, for example, that of Mayr (1942, p. 120), who says: "Species are groups of actually or potentially interbreeding populations which are reproductively isolated from other such groups." It should be noted, however, that a species may consist of a *single* population of individuals. In short, a species is a single population or a series of populations of individual organisms; and, just as no two single individuals are just alike, so, no two populations of individuals are identical. Just as no single all-inclusive definition of species has been found, so, no single criterion for distinguishing between species has been agreed upon. Because of the endless differences in degree of differentiation within the individual organism, ranging from that of the simplest to the most complex, decisions concerning just how much difference between populations shall be sufficient for the recognition of a new species had best be left to the judgment of biosystematists who specialize in the various fields of organic life.

Fundamental to the recognition of kinds or types of species among the flowering plants is the fact that species are perpetuated by the reproduction of individuals and that the possible methods of reproduction are definitely limited. This important fact sets up conditions making for resemblances and differences between species. Furthermore, each species originates, perpetuates itself for a limited period, and disappears. At different stages in its life history it will present very different aspects according to its success in competing with other organisms and with the inanimate environment. Thus, the method of reproduction and the stage of development of a species are two factors which determine the aspect of a species at a given time.

Another important factor in determining kinds of species is the type of genetic system which operates in the perpetuation of the species. This depends on many other things in addition to the method of reproduction. If the method of reproduction is sexual, then the fertility relations between the individuals or between intra-specific groups will certainly affect the type of the population. The chromosome situation in the species is another important genetic factor affecting type of population, since the individuals may be diploid, polyploid, allopolyploid, euploid, or dysploid, or a mixture of two or more of these conditions.

Based on such considerations as the foregoing, Camp and Gilly (1943) have introduced a clearly defined series of categories of species, under which it is possible to classify at least provisionally all the species of *Crepis*. But until more information is available, the classification of many of the species under these categories must remain only tentative. Accordingly, the simple scheme of classification shown in table 1 is presented mainly for the purpose of giving a picture of the nature of the species populations existing in this genus. In addition, classification according to Camp and Gilly's categories is incorporated into this representation by the capital letter or letters following each species. When the classification is tentative or doubtful, which is often true, the letter is followed by a question mark. The section in which each species belongs is shown by the number preceding it. The definitions of such of Camp and Gilly's categories as apply to *Crepis* and the letters designating them are as follows:

Homogoneon: a species which is genetically and morphologically homogeneous, all members being interfertile (H).

Paragoneon: a species with relatively little morphological or genetical variation throughout its range, but which contains some aberrant genotypes; all its individuals are interfertile (P).

Rheogameon: a species composed of segments of reasonably marked morphological divergence the distributions of which are such that gene interchange may take place in sequence between them; individuals of contiguous segments are interfertile (R).

Dysploidion: a species composed of morphologically similar members of a dysploid series (for example, 10, 11, 12, 13, ...) the individuals of which are sexually reproductive (D).

Euploidion: a species the individuals of which are sexually reproductive and which is composed of segments with a common origin arranged in a euploid series (such as 8, 16, ...); the segments are morphologically separable and, although similar in appearance, because of differential responses in various environments, seem to intergrade (E).

Allopoloidion: a species derived by allopolyploidy; its individuals, although usually highly variable, are interfertile (A).

Apogameon: a species containing both apomictic and nonapomictic individuals (Ap).

From the rare occurrence of the index letters D, E, and A in table 1, it will be obvious that almost all *Crepis* species are believed to consist entirely of diploid individuals. But at the same time, it must be noted that occasional aberrant individuals with slight deviations from the diploid number of the species are liable to be found in any species. These, however, have little if any permanent effect on the genetic system of the species. Inability to classify a species definitely in one of Camp and Gilly's categories is, of course, due to lack of definite information. The actual

TABLE 1

CLASSIFICATION OF 196 SPECIES OF CREPIS IN ACCORDANCE WITH METHOD OF REPRODUCTION AND
DEGREE OF COMPLEXITY
(Each species is preceded by its section number.)

REPRODUCTION SEXUAL SO FAR AS KNOWN.—MONOMORPHIC SPECIES

Known at present from only one or very few stations

1. C. geracioides...	P ?	10. C. khorassanica.....	H ?
4. C. albiflora...	H ?	10. C. taygetica.....	H ?
4. C. dioritica.....	P ?	10. C. Guilioliana.....	H ?
5. C. willemetioides...	H ?	10. C. crocifolia.....	H ?
8. C. kilimandscharica.....	H ?	10. C. athoa.....	H ?
8. C. keniensis.....	H ?	11. C. Schachtii.....	H ?
8. C. suffruticosa.....	H ?	11. C. Faureliana.....	H ?
8. C. iringensis.....	H ?	11. C. demavendi.....	H ?
8. C. cameroonica.....	H ?	12. C. alaica.....	H ?
8. C. urundica.....	H ?	12. C. naniforma.....	H ?
8. C. chirindica.....	H ?	14. C. ircutensis.....	P ?
8. C. congoensis.....	H ?	16. C. connexa.....	H ?
8. C. caudicalis.....	H ?	16. C. elbrusensis.....	H ?
8. C. glandulosissima.....	H ?	19. C. amanica.....	H ?
8. C. ugandensis.....	H ?	20. C. eritreensis.....	H ?
8. C. simulans.....	H ?	20. C. tybakiensis.....	H ?
8. C. Gossweileri.....	H ?	21. C. Gmelini.....	H ?
8. C. Friesii.....	H ?	24. C. insignis.....	H ?
8. C. Mildbraedii.....	H ?	25. C. Fontiana.....	P ?
8. C. Bruceae.....	H ?	25. C. canariensis.....	P ?
10. C. Strausii.....	H ?	25. C. Balliana.....	H ?
10. C. darvasica.....	H ?	25. C. Claryi.....	H ?
10. C. ciliata.....	P ?	26. C. atheniensis.....	H ?
10. C. bertisceae.....	H ?	26. C. Muhlisii.....	H ?
10. C. albanica.....	H ?	27. C. Forskalii.....	H ?
10. C. dens-leonis.....	H ?	27. C. filiformis.....	H ?

Known from several or many stations

1. C. viscidula.....	H ?	11. C. Robertioides.....	P ?
2. C. kashmirica.....	P ?	11. C. abyssinica.....	H ?
4. C. terglouensis.....	P ?	12. C. corniculata.....	P ?
4. C. rhaetica.....	P ?	12. C. lactea.....	H ?
4. C. hokkaidoensis.....	H ?	12. C. elegans.....	P ?
4. C. polytricha.....	P ?	13. C. gymnopus.....	H ?
5. C. lapsanoides.....	P ?	13. C. praemorsa.....	P ?
5. C. lyrata.....	P ?	14. C. Bungei.....	P ?
5. C. hierosolymitana.....	P ?	16. C. sahendi.....	P ?
6. C. pontana.....	P ?	17. C. napifera.....	P ?
8. C. Schultzii.....	H ?	19. C. Stojanovi.....	P ?
8. C. subscaposa.....	P ?	19. C. pterothecoides.....	P ?
10. C. songorica.....	P ?	20. C. syriaca.....	D, P ?
10. C. chondrilloides.....	P ?	20. C. Schimperii.....	H ?
10. C. auriculaefolia.....	P ?	21. C. elongata.....	H ?
10. C. Baldaccii.....	H ?	23. C. patula.....	P ?
10. C. Pantocsekii.....	H ?	23. C. Zacintha.....	P ?
10. C. Sibthorpiana.....	H ?	24. C. cretica.....	P ?
10. C. incana.....	P ?	24. C. apula.....	H ?
11. C. pinnatifida.....	H ?	24. C. Suffreniana.....	P ?
11. C. bithynica.....	P ?	25. C. spatulata.....	H ?
11. C. tenerima.....	H ?	25. C. Clausonis.....	P ?
11. C. xylorrhiza.....	H ?	25. C. Noronhaea.....	P ?
11. C. Hookeriana.....	P ?	25. C. libyca.....	P ?

TABLE 1—(Continued)

REPRODUCTION SEXUAL SO FAR AS KNOWN.—POLYMORPHIC SPECIES

One or more minor variants recognized

1. <i>C. sibirica</i>	P ?	12. <i>C. flexuosa</i>	P ?
1. <i>C. paludosa</i>	P ?	13. <i>C. incarnata</i>	P ?
4. <i>C. Jacquini</i>	P ?	14. <i>C. tectorum</i>	P
4. <i>C. chrysantha</i>	P ?	16. <i>C. purpurea</i>	P ?
5. <i>C. smyrnaea</i>	P ?	16. <i>C. frigida</i>	P ?
5. <i>C. mollis</i>	P ?	19. <i>C. palaestina</i>	P
5. <i>C. montana</i>	P ?	20. <i>C. alpina</i>	P ?
5. <i>C. Mungierii</i>	P	20. <i>C. rubra</i>	P
6. <i>C. conyzaefolia</i>	P ?	20. <i>C. Kotschyana</i>	P
6. <i>C. blattarioides</i>	P ?	20. <i>C. Thomsonii</i>	P ?
7. <i>C. achyrophoroides</i>	P ?	21. <i>C. tibetica</i>	P ?
7. <i>C. elymaitica</i>	P ?	23. <i>C. multiflora</i>	P
8. <i>C. alpestris</i>	P ?	24. <i>C. nicaeensis</i>	P
8. <i>C. meruensis</i>	P ?	24. <i>C. capillaris</i>	P, E ?
8. <i>C. carbonaria</i>	P ?	24. <i>C. parviflora</i>	P
8. <i>C. Ellenbeckii</i>	P ?	24. <i>C. neglecta</i>	P
8. <i>C. Swynnertonii</i>	P ?	24. <i>C. corymbosa</i>	P ?
9. <i>C. tingitana</i>	P ?	24. <i>C. fuliginosa</i>	P
9. <i>C. leontodontoides</i>	P	25. <i>C. Salzmannii</i>	P ?
10. <i>C. sonchifolia</i>	P ?	25. <i>C. Bourgeauii</i>	P ?
10. <i>C. biennis</i>	P, A ?	25. <i>C. divaricata</i>	P ?
10. <i>C. pannonica</i>	P ?	25. <i>C. Marschallii</i>	P
10. <i>C. latialis</i>	P ?	26. <i>C. juvenalis</i>	P ?
10. <i>C. turcica</i>	P ?	26. <i>C. aculeata</i>	P ?
10. <i>C. Triasii</i>	P ?	26. <i>C. amplexifolia</i>	P ?
10. <i>C. Raulini</i>	P ?	26. <i>C. aspera</i>	P
10. <i>C. macropus</i>	P ?	27. <i>C. Rueppellii</i>	P ?
10. <i>C. oporinoides</i>	P ?	27. <i>C. bellidifolia</i>	P
10. <i>C. turcomanica</i>	P ?	27. <i>C. bursifolia</i>	P
11. <i>C. oreades</i>	P ?	27. <i>C. nigricans</i>	P ?
11. <i>C. crocea</i>	P ?, A ?	27. <i>C. senecioides</i>	P

Two or more subspecies exist

3. <i>C. pygmaea</i>	R ?	12. <i>C. nana</i>	R
4. <i>C. aurea</i>	R	15. <i>C. runcinata</i>	R
7. <i>C. albida</i>	R ?	19. <i>C. Reuteriana</i>	R
8. <i>C. hypochaeridea</i>	R ?	19. <i>C. pulchra</i>	R
8. <i>C. Newii</i>	R ?	20. <i>C. foetida</i>	R
8. <i>C. scaposa</i>	R ?	21. <i>C. multicaulis</i>	R
9. <i>C. suberostris</i>	R	22. <i>C. sancta</i>	R
10. <i>C. bupleurifolia</i>	R ?	23. <i>C. Dioscoridis</i>	R
11. <i>C. heterotricha</i>	R ?	25. <i>C. vesicaria</i>	R, E
11. <i>C. armena</i>	R ?	26. <i>C. setosa</i>	R

REPRODUCTION APOMITIC, AT LEAST PARTLY.—MONOMORPHIC SPECIES

18. *C. chloroclada*..... Ap ?

(Table 1 is concluded on the next page)

TABLE 1—(Concluded)

POLYMORPHIC SPECIES	
With numerous forms	With both subspecies and forms
15. <i>C. monticola</i> A, E, Ap	15. <i>C. occidentalis</i> A, E, Ap
15. <i>C. pleurocarpa</i> A, E, Ap	15. <i>C. Bakeri</i> A, E, Ap
15. <i>C. intermedia</i> A, E, Ap	15. <i>C. modocensis</i> A, E, Ap
15. <i>C. barbiger</i> a A, E, Ap	15. <i>C. acuminata</i> A, E, Ap
18. <i>C. Phoenix</i> A ?, E ?, Ap ?	15. <i>C. atribarba</i> A, E, Ap
18. <i>C. Bodinieri</i> A ?, E ?, Ap ?	18. <i>C. rigescens</i> A ?, E ?, Ap ?
18. <i>C. lignea</i> A ?, E ?, Ap ?	

amount of morphological variation in a species may be very different from that indicated by the limited number of herbarium specimens at present available. Fertility relations among the individuals have not yet been tested in most of the species. Although fifty-five different species have been used in experiments on interspecific hybrids, most of them have not been subjected to intraspecific genetic analysis. For these reasons the classification into the first three of Camp and Gilly's categories must usually be tentative and be based on admittedly inadequate information. But it seemed worth while to attempt such classification, for the purpose of giving as complete a picture as possible of the kinds or probable kinds of species comprising this genus.

It should be emphasized that in classifying about one-half of the total species as monomorphic, both in table 1 and in the species descriptions, there is no intention on the part of the present author to imply that this classification is permanent. This monograph attempts to represent the genus as it is known at present, and the author is well aware that further collections may change the status of any of these "monomorphic" species. Similarly, the status of some of the polymorphic parageneons may be changed to that of rheogameons. But those which are now recognized as rheogameons will undoubtedly remain in that category, unless some future taxonomist can show good reasons for raising certain subspecies to the rank of species. It is certain, however, that the preparation of table 1 will have been worth while if it helps to correct the unfortunate impression given by Huxley (1943) that *Crepis* is a characteristically apomictic genus. The morphological peculiarities indicating polyploidy and apomixis are fairly reliable (cf. Part II, secs. 15 and 18), and it can be definitely stated that almost all of the species in the genus are not characterized by such peculiarities. In other words, all but a few of the species of *Crepis* are characterized by diploidy and by syngamy.

In the nine American species of section 15 which are known to be partly apomictic, evolution and differentiation have been determined by hybridization and polyploidy, as well as by apomixis. The resulting populations may be described as heteroploid, agamic complexes. Compared with homoploid populations, such complexes show great variability and taxonomic diversity, especially in regions where two or more of the original diploid forms occur. The application to such complexes of the usual criteria on which the species concept is based indicates that, in these complexes, there are no entities that are homologous with species which consist of homoploid sexual groups. Hence, a systematic treatment of this type of complex was proposed by Babcock and Stebbins (1938) in which species and subspecies are recognized chiefly on the basis of the distinctions between the diploid sexual forms. A large number of *formae apomicticae* which have no taxonomic status are described to

cover the individual biotypes perpetuated by apomictic reproduction. A few of these *formae apomicticae* are mentioned in the taxonomic treatment of section 15 in Part II of this monograph.

The classification of sexual, homoploid populations as species or subspecies primarily or crucially on the basis of the degree of intersterility or interfertility demonstrated by experimental crosses, as suggested by Clausen, Keck, and Hiesey (1939), has not been adopted in *Crepis*. In the first place, it was impracticable for obvious reasons, and, secondly, the general consensus among plant systematists is opposed to it. The present author had to face this question in deciding on the disposition of *Crepis foetida* and its two closest relatives, *C. eritreënsis* and *C. Thomsonii* (Babcock, 1938). The last two are geographically isolated from the first, and they differ from it and from each other in morphological and physiological characters which are sufficient, in my opinion, to warrant their recognition as species, even though artificial hybrids between them were rather highly fertile. The recognition of *C. Thomsonii* and *C. eritreënsis* as species is in agreement with the principles advocated by Huxley (1940, p. 22), as follows: "As Turrill (cf. Huxley, 1940, pp. 60–68) has emphasized, the fact that groups may or might show fertile intercrossing when artificially or in other ways secondarily brought together does not disprove their right to be styled species. It is the actual facts of nature, not its every potentiality, with which the systematist has to deal. The fact of their separate existence *qua* self-perpetuating interbreeding groups, together with *either* a reduction or absence of fertility in intercrossing, *or* a certain empirically evaluated degree of morphological or physiological characters, should be taken as the basis of decision."

In working out the classification of *Crepis* it was practically impossible to apply on an extensive scale the excellent methods of experimental taxonomy developed by Clausen, Keck, and Hiesey (1940). Hence, the four biosystematic units which they have adopted (Clausen, Keck, and Hiesey, 1945), namely, ecotype, eco-species, cenospecies, and comparium, are seldom mentioned in the present work. In the discussion of certain *Crepis* species, however, reference is made to ecotypes which are "genetically and physiologically distinct ecologic races." Furthermore, according to Clausen, Keck, and Hiesey (*loc. cit.*), "the ecospecies approximates the species of moderately conservative taxonomists working along conventional lines." As for cenospecies and comparia, "species entirely unable to exchange genes with each other belong to different cenospecies"; whereas "distinct cenospecies which are still able to produce first generation hybrids with one another belong to one comparium." On this basis, in *Crepis*, the same comparium may include such widely separated species (cenospecies) as *C. paludosa* (sec. 1) and *C. lybica* (sec. 25), *C. aurea* (sec. 4) and *C. vesicaria* (sec. 25), *C. leontodontoides* (sec. 9) and *C. bursifolia* (sec. 27), or *C. pannonica* (sec. 10) and *C. aculeata* (sec. 26).

In contrast with the foregoing comparia are certain groups of species which belong in the same section but which also produce sterile hybrids (see pp. 58–59). For example, in section 20, six of the fifteen interspecific combinations produced vigorous but *sterile* hybrids. Five of these were crosses between various 5-paired species and the 4-paired *C. Kotschyana*. It has been shown (Sherman, 1946) that the inclusion of this 4-paired species in the same section with a number of 5-paired species, *primarily on morphological grounds*, is strongly supported by cytogenetic evidence. The meiotic behavior of the chromosomes in F_1 hybrids having *C. Kotschyana* for one parent and any other member of the same section for the other parent strongly indicates that all of these species must have been derived immediately from a common 5-paired ancestor. Therefore, they comprise a close group

and are properly classified in one section. But, on the sole basis of hybrid sterility, this one section is a comparium.

Thus, if we consider hybrid sterility alone, we are compelled to recognize, as comparia, groups of extremely close and relatively remote species within the same genus. Hence, the category "comparium" signifies nothing more definite than classification in the same genus, together, as a rule, with a type of genetic relationship which happens to make sterile hybrids possible. It is another illustration of the inadequacy of a single criterion to serve as the basis for the systematic classification of organisms. Nevertheless, the potential value of experimental genetics in working out many of the unsolved problems in this genus should not be overlooked. For example, the true status of the Caucasian forms of *C. paludosa* (see Part II, p. 235) or of the Uganda assemblage of variants included under *C. Rueppellii* (see Part II, p. 897) can probably be determined only by such methods.

Concerning the natural species recognized in the present treatment of *Crepis*, however, the author believes that they all probably conform to the two fundamental principles governing the existence and distribution of wild plants which are formulated by Clausen, Keck, and Hiesey (*loc. cit.*), as follows:

- 1) Natural species consist of individuals whose genes are in internal balance so that a harmonious development is assured generation after generation.
- 2) The individuals of wild species are not only balanced internally, but fit their natural environment; they are in rhythm with the seasons and adapted to the over-all conditions of temperature, moisture, wind, soil and light, as well as to the biotic elements of their environment.

At the same time it is frankly admitted that the twenty species of *Crepis*, each of which is known at present only from a single specimen or one small collection, have been recognized as species merely because their morphological distinctness and peculiarities make them unclassifiable under any other species. It remains for the future to discover whether they actually represent populations which conform to the two principles quoted above, and to the six basic criteria defined on page 34.

New species.—It has been found to be necessary or desirable to describe a total of thirty-three new species, fifteen of which are first published in this monograph. Of the total number, eight are based on a single specimen. In the opinion of the present author it is desirable to place these on record, because of the strong likelihood that each specimen actually represents at least one natural population. Some of them, like *C. Schachtii*, *C. Guioliana*, and *C. Balliana*, are of special interest because of their phyletic relations.

SUBGENERIC CATEGORIES

In all of the earlier publications on the cytotaxonomy of *Crepis* (especially that of Babcock and Cameron, 1934), it was assumed that the three principal subdivisions of the genus which were recognized by Bentham and Hooker (1873–1876), namely, *Catonia*, *Eucrepis*, and *Barkhausia*, could be treated as subgenera. However, it became clear later that such groups cannot be recognized as natural subdivisions of the genus. This conclusion was supported by the evidence from geographic distribution, since representatives of these groups, as defined by Bentham and Hooker, occur together throughout almost the entire range of the genus. Therefore, the present arrangement of the species in twenty-seven sections was adopted as a truly natural classification. Although the sections can be grouped roughly into three divisions, namely, primitive, intermediate, and advanced, yet an attempt to key out all the species into one or another of those three major groups would be just as futile as the earlier attempts to classify them under *Catonia*, *Eucrepis*, and *Barkhausia*.

SUBSPECIFIC CATEGORIES

Early in his taxonomic experience the present author was impressed by Dr. H. M. Hall's arguments for the recognition of subspecies as the only subspecific categories worthy of receiving Latin names to be used in taxonomy. Although fully aware of the needs for names of some sort for lesser systematic units for genetical and other purposes, Hall maintained that there was no justification for encumbering the taxonomic literature and indexes with Latin names of units lower than the subspecies (Hall, 1926). Accordingly, at the outset of my work on *Crepis* it was decided that the only subspecific category to receive Latin names would be subspecies and that entities and forms of lower rank would be given numbers in the order of their discovery. Therefore, such entities and forms are listed in the taxonomic descriptions as numbered "minor variants." Whenever these entities or variants have been given names in earlier publication, the names are cited as synonyms in parentheses following the numbers, and, when the names were in the category of species, they are also included in the synonyms listed under the species descriptions. An increasing trend in taxonomic practice in the direction advocated by Hall has been evident. The recent papers of Clausen (1941) and Camp and Gilly (1943) give adequate support to this procedure.

Ideally, a subspecies is an intraspecific population with a geographic distribution which is partly isolated from that of the rest of the species but which overlaps more or less the distribution of one or more other subspecies. It may comprise one or numerous ecotypes. A species consisting of two or more subspecies is, in the sense of Rensch (1929), a *rassenkreis*, or, as defined by Camp and Gilly (1943), a *rheogameon*, or, as named by Clausen, Keck, and Hiesey (1945), an *ecospecies*. All of the polymorphic species listed in table 1 which are followed by the letter R are known to be of this type. Those followed by R? may be of this type, but available data are not sufficient to permit definitely saying so. In these and in a few species presenting special problems, such as *C. Dioscoridis* (see Part II, p. 746), the recognition of subspecies has been deemed necessary or warranted, even though the species as a whole is not a typical *rheogameon*.

In this brief discussion of taxonomic concepts, emphasis has been given to the need for a realistic view of natural populations of organisms. At the same time, recognition has been given to the difficulties arising in an attempt to make a natural classification of such populations even within a single genus. Importance is attached to a sound basis for delimiting genera and species. The classification presented in table 1 shows the kinds of species comprising the genus *Crepis*.

CHAPTER 3

CRITERIA OF CLASSIFICATION AND PHYLOGENY

THE PRINCIPAL CRITERIA for classification of the species into sections are the data on comparative morphology, chromosome number and morphology, genetics, cytogenetics, and geographic distribution. The evidence on geographic distribution is reviewed in chapter 5. Before discussing the morphologic, cytologic, and genetic criteria, the significance in this genus of the general habit of the individual plant deserves consideration. All numbered figures cited in this chapter are in Part II.

HABIT OF THE PLANT

The 196 species of *Crepis* are all herbs, unless *C. kilimandscharica* (fig. 57) might be considered a subshrub. This forestal plant develops a woody stem or caudex up to at least 1.3 meters in height and produces the usual rosette of caudical leaves at the summit. Each year the caudex is lengthened, a new rosette of caudical leaves is produced, and later the flowering stem appears. This species, therefore, in the terminology of Raunkiaer (1937), must certainly be classed as a chamaephyte. Several other perennial species develop a short, woody caudex which persists above ground. Good examples are *C. albida* subsp. *asturica* (fig. 47), *C. suffruticosa* (fig. 60), and *C. caudicalis* (fig. 73). Others sometimes develop a relatively thick, much-branched caudex at the ground level, as in *C. oporinoides* (fig. 121) and *C. xylorrhiza* (pl. 10). All such species may be considered as chamaephytes. But most of the perennial *Crepis* species are hemicryptophytes. That is, they have a perennial caudex which persists at or just below the surface of the soil, producing one or more new flower stems each year. In a few species subterranean shoots are generated, and such species may be classed as geophytes. Examples are *C. nana* and other species in section 12, *C. occidentalis* and other members of section 15, *C. frigida* and *C. elbrusensis* of section 16.

There are 143 species which are true perennials, many of which are probably short lived, and 40 species which are strictly annual plants. The other 13 species are variable with respect to duration of life, some (*C. biennis*, *C. nicaeënsis*) being characteristically biennial but occasionally flowering the first season from the seed, whereas several species in section 25, including the polymorphic *C. vesicaria*, vary from perennial to annual. That the annual type has been derived from the perennial type in this genus is beyond question. Evidence on degree of reduction of the plant and its parts and on progressive adaptation to a more and more xerophytic environment, together with the well-established facts concerning phylogenetic changes in the chromosomes, all point definitely to this conclusion (see tables 2 and 11). That this relationship resembles that found in many other natural groups is shown by Hutchinson's (1926, p. 6) generalization: "Perennials are older than biennials, and from them annuals have been derived." Hutchinson (*loc. cit.*) also states that: "In certain groups, trees and shrubs are probably more primitive than herbs," a relationship which is certainly indicated in *Crepis*.

MORPHOLOGIC CRITERIA

The parts of the plant which have been found to be most useful in classification will now be discussed, with occasional allusions to the phylogenetic significance of certain resemblances and differences.

Rhizome versus taproot.—Most of the perennial species are easily classified in one or another of two distinct groups, namely, those with a rhizome which has the

gross morphology of a stem and those with a deeply penetrating true root with a central stele. There are a few species which have been placed in the second group but which appear to be intermediate, for example, *C. leontodontoides* of section 9 and *C. Reuteriana* of section 19. Such species, however, have either a deeply penetrating root, at least in some specimens, or an underground stem. The most primitive species in the genus, as determined from other morphological characters and their chromosomes, all have a rhizome. However, one species which has been placed in the first group actually appears to demonstrate the specialization of the rhizome to function as a taproot. In *C. rhaetica* the young plants have a short vertical rhizome which gradually lengthens into a deeply penetrating one simulating a taproot. (See Part II, p. 253.) The existence of such intermediate species as *C. rhaetica* and the two mentioned above is considered to support the hypothesis that, in *Crepis*, the taproot type developed from the rhizome type, an assumption which is discussed further under phylogeny (p. 65).

Caudex.—The caudex is that part of the plant which is intermediate between the root (or the rhizome) and the flower stem. In the typical hemicryptophytes and in the annuals the caudex is relatively short. It bears the earlier leaves of the season's growth preceding development of the flower stem. But in many of the perennial species, especially in those of the deep-rooted type, the caudex becomes elongated in older plants. It then usually bears either leaf scars or the old bases of the leaves of previous years. In those rare herbarium specimens which were so carefully collected as to preserve a part if not all of the main root, it is sometimes possible to estimate the plant's age from the consecutive series of leaf scars. Mat-forming species, such as *C. xylorrhiza*, have a caudex with several branches. In a few species these are much elongated (see *C. frigida*, Part II, fig. 189); and in certain others the plant spreads by stolons or adventitious buds on the fibrous roots, as in *C. pygmaea* (Part II, fig. 20), *C. Bungei*, and several members of section 12.

Caudical leaves.—The caudical leaves usually form a rosette with the leaves, at least the lower ones, lying on the ground. In many species the whole rosette is flat and symmetrical, but in others the younger caudical leaves are semierect. In shape, the caudical leaves range from broadly elliptic to narrowly lanceolate or almost linear; but by far the most common shape is oblanceolate. They are generally petiolate. In outline they may be entire, dentate, lyrate-pinnatifid, runcinate, or deeply pinnatifid, with broad or narrow segments. All four species in section 1 have coarsely dentate or sublyrate caudical leaves; but in *C. kashmirica* (sec. 2) they are almost entire, and in *C. pontana*, the most primitive deep-rooted species, they are entire. In the genus *Dubyaea*, the putative ancestors of *Crepis*, both entire and lyrate caudical leaves occur in different species. It is impossible to say, therefore, that one form of caudical leaf is more primitive than another. It is worth noting, however, that the lyrate pattern is of common occurrence in this genus and that it sometimes appears, as in *C. pannonica* for example, in the earliest caudical leaves but fails to appear in the later ones. In this connection the author has observed a seedling character of considerable interest. In most of the species the earliest leaves radiate symmetrically, but in *C. sibirica* and several other primitive species they are definitely congested into two groups on opposite sides of the stem. This seedling character has also been observed in *C. pannonica* of section 10. Furthermore, it has been observed that although the form of the leaves on an individual plant may be profoundly altered by a sudden, extreme change in temperature, yet plants of different species produce the characteristic form and relative size of the leaves of each species when grown under uniform, favorable greenhouse or garden conditions. Under such conditions the caudical leaves, when used

along with other characters, provide dependable criteria for classification of cultivated specimens.

Stem.—In most species of *Crepis* the stem is erect or semierect and more or less branched, with a leaf or bract subtending each branch and with several or many flower heads. The type of branching, often being distinctive, provides a good diagnostic character (see figs. 57, 67, 80). But in certain sections the species are all characterized by having scapiform, that is, one-headed stems bearing few or no leaves (see secs. 4 and 11). In some of the advanced sections, especially section 27, there is a strong tendency for the plant to have several slender, flexuous stems. In the species with branched stems the main branches may be disposed paniculately, racemously, or dichotomously; but the general plan of the inflorescence is that of a simple or compound cyme. Thus, there are many combinations of characteristic stem and branching types which are of value in classification.

Cauline leaves.—As a general rule, in the species with branched stems, the cauline leaves are gradually reduced from the base of the stem upward, but, in this, there is one outstanding exception (see sec. 18). In the more primitive species which are characterized by having cauline leaves these leaves are relatively large (see figs. 14, 23, 94). But in the advanced species they are usually extremely reduced (see figs. 240, 258, 304). The lowest cauline leaves generally exhibit intergradation in shape between the petiolate oblanceolate caudical leaves and the sessile, lanceolate middle cauline ones. In many species the middle cauline leaves are amplexicaul, that is, they clasp the stem, and the base is often sagittate or auriculate; also, various modifications of these characters occur. The uppermost leaves are usually bractlike.

Peduncles.—The peduncles, in species of branching habit, vary greatly in length and thickness in different species. For examples illustrating the greatest extremes of difference, compare *C. geracioides* (fig. 14) with *C. aspera* (fig. 291), or *C. Dioscoridis* subsp. *tubaeformis* (fig. 247) with *C. Zacintha* (fig. 249). The difference in the general aspect of the plant caused by these variations is tremendous. Another distinctive feature of the peduncle in some species is its inflation toward the base of the flower head; this is well shown in *C. Dioscoridis tubaeformis*, whereas in many species it remains about the same diameter throughout.

Flower heads.—The flower heads are commonly described as large, medium, or small; but, it being necessary in critical determinations to depend on actual measurements and other details of the involucre, these vague terms are of little value. Reduction in size of the flower heads has gone along with reduction in size of other plant parts in association with progressive advancement and specialization in this genus. But the number of florets in the heads has not followed any such consistent trend. The average number of florets in a head, however, is a useful character in distinguishing certain sections and species. Data regarding this are provided so far as possible in the descriptions in this monograph. Another feature which sometimes serves to distinguish between species is the position of the young flower heads before anthesis. In certain species they are always bent downward, that is, they are "nodding"; this is caused by the curvature of the peduncle or of the branchlet bearing two or three heads. But in certain species, for example *C. foetida* and *C. rubra*, the individual plants of a single subspecies or strain may vary in this respect. This difference in position of the young heads in the two species mentioned was found to depend on a single gene difference.

Involucre.—Differences in the involucre are among the most useful for purposes of classification and identification, as well as for establishing phylogenetic relations. In *Crepis* the involucre consists of two distinct series of scales which are called the outer and inner bracts of the involucre. In many species some of the outer bracts

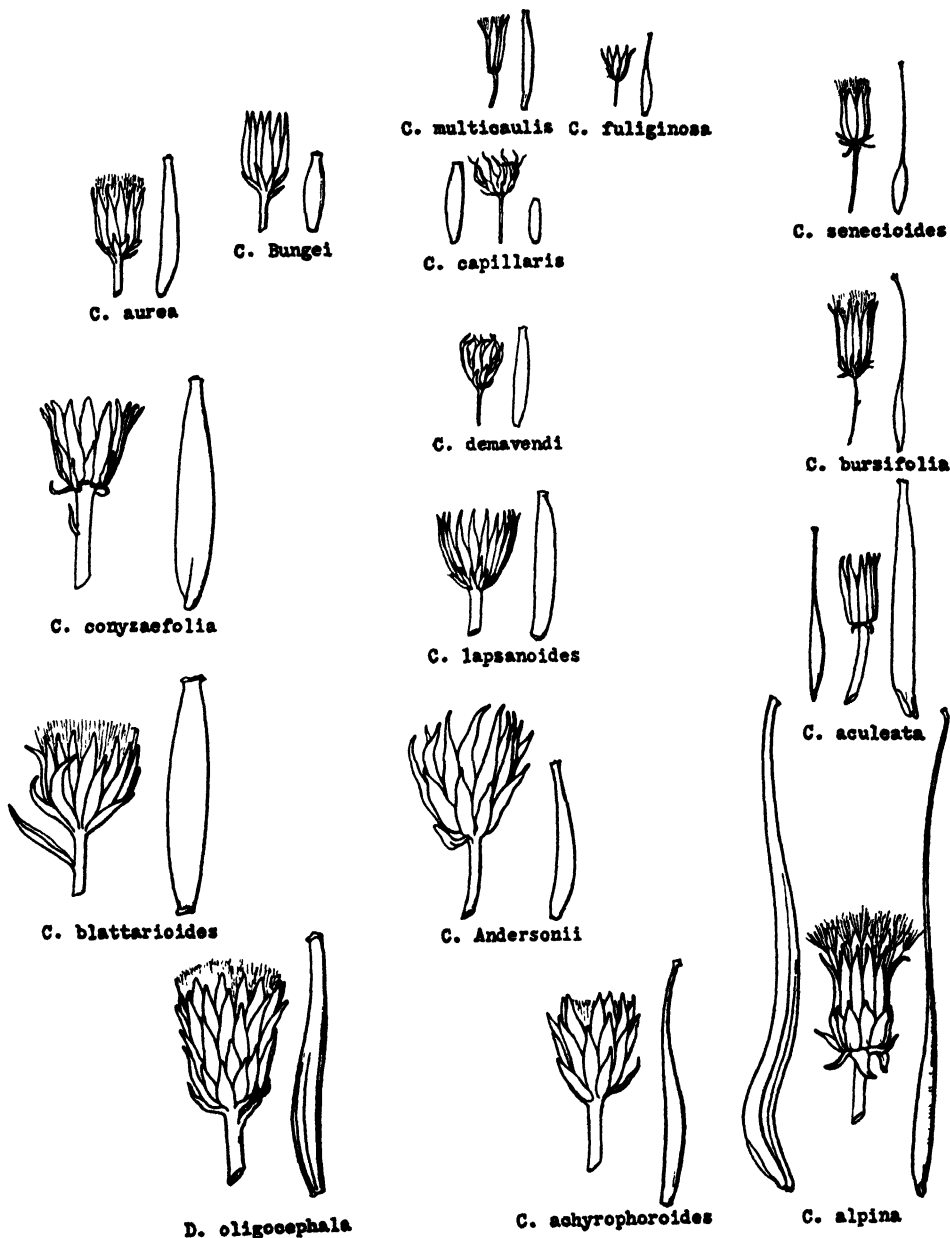


Fig. C. Fruiting heads and achenes of *Dubyaea oligocephala* and of 15 species of *Crepis* arranged in evolutionary series to show progressive reduction in size of involucre, number of bracts, and relative size of the outer bracts, as well as size of achenes, dimorphic achenes (*C. albida* and *C. aculeata*), and development of beaked achenes. (Note the extreme contrasts between the most primitive type, *D. oligocephala*, and the most advanced species, *C. fuliginosa*, *C. bursifolia*, and *C. senecioides*.)

approach the inner ones in length, so that in an immature involucre the combined series appear as one. In addition, the outer bracts in some species are broad and overlapping or imbricate (see *C. achyrophoroides* and *C. alpina*, fig. C, lower right). A fully imbricate involucre is found in that species of *Dubyaea* (*D. oligocephala*,

fig. C, lower left) which most resembles *Crepis* in several other characters. This led Schultz Bipontinus to place *D. oligocephala* with *C. albida* in Cassini's genus *Paleyia*. But, in *C. albida*, when the flower head matures, the outer and inner series of bracts become clearly differentiated, as in *C. achyrophoroides* and *C. alpina*, and in some of the subspecies of *C. albida* the two series are distinct before anthesis.

Considering the genus as a whole, it can be said that there is a general trend in reduction of the involucre in passing from the most primitive to the most advanced species. This reduction affects the total size of the involucre, the total number of bracts, and the relative size of the outer bracts, aspects of which are clearly illustrated in fig. C.

In addition to reduction, phylogenetic advancement in this genus is also accompanied by two distinct kinds of specialization. The most common form of specialization consists of a dorsal thickening of the inner bracts. As a result, in the mature involucre, each inner bract has a definite keel, extending from the base toward the apex, which is either narrow, making it carinate, or broad, making it navicular. This keel consists of a mass of parenchymatous cells; and such a bract is referred to as spongy-thickened. In contrast with these specialized types, the involucreal bracts in the most primitive species remain essentially unchanged in fruiting heads, except that they often become indurate. The primitive type of involucre in *C. sibirica* (fig. 13, *b*) should be compared with the navicular type shown in *C. juvenalis* (fig. 287, *g, h*) and with the carinate type illustrated by *C. amplexifolia* (fig. 289, *o*). In many of the more advanced species the parenchymatous thickening extends into the receptacle, so that the whole lower part of the involucre becomes swollen. The keels and swollen base are usually paler in color than the rest of the involucre (see frontispiece, *C. suberosistris*). The fact that in the primitive species of *Crepis* the involucre is seldom, if ever, reflexed at maturity so as to expose the ripe achenes, whereas in the advanced species the mature involucre is commonly reflexed, makes it very probable that the kind of specialization above described is actually an adaptation for more efficient seed distribution by the wind.

The other kind of specialization is much less common. In fact, it is strongly developed only in section 23. The four species in this group are more similar to one another than to any other species in the genus; yet they exhibit such remarkable diversity that a superficial view would lead to the assumption that they are not closely related. In fact, the most advanced member of the group has, until now, been considered a distinct genus (*Zacintha*). This is a weed spread widely over southern Europe, whereas the most primitive member, *C. patula* (which has also been treated as a separate genus by some taxonomists), is endemic in Algeria and Tunisia. By comparing these two species (figs. 242, *l, m*, and 249, *g, k*) their common type of involucreal specialization is evident. In both species the inner involucreal bracts are never reflexed, but they become much thickened and strongly indurate, so that the mature achenes are firmly enclosed. Just why this form of specialization should have proved advantageous to the species is not clear, but in *C. patula* it is associated with the possibility of distribution by running streams. One of the other two species in this section, *C. Dioscoridis* (figs. 243–247), is intermediate between the two extremes in many characters, including the involucreal thickening.

Receptacle.—The receptacle, in mature involucre, provides several characters of value in classification. The surface is flat or slightly convex and is either areolate (with nearly equal small areas, each with a stipule near the center where the achene was attached), or alveolate (with the areoles separated by a ridge or fringed membrane, that is, fimbriate), or the fimbriae may be replaced by paleae. The paleae may be either bristlelike (setiform), as in sections 18 and 22, or flattened

and membranous, as in *C. foetida* subsp. *commutata*. Except for those in the two small sections and the one subspecies just mentioned, the receptacle is epaleaceous in *Crepis*. The fimbriae on alveolate receptacles, however, are often ciliate or strigose, sometimes conspicuously so.

Florets.—The complete individual floret consists of the inferior ovary, with the tubular and ligulate corolla bearing the anther tube attached by its five filaments and surrounding the style and style branches, which are pushed up through the anther tube in anthesis. The ovary is minute and superficially similar throughout the genus. Further light on the phylogenetic relations of some of the most primitive species may be obtained by a detailed study of the vascular anatomy of the ovary. In a survey of ovary anatomy in the Cichorieae, made in connection with his monograph on *Dubyaea* and *Soroseris*, Stebbins (1940) found that a number of species of *Crepis*, including several primitive ones, have a more reduced floral anatomy than the more primitive species of *Dubyaea* (see appendix 4, pp. 169–170).

The corolla provides the following useful characters: total length, width of ligule, color of ligule, length of ligule teeth, relative length of the tube, and pubescence on the tube and base of ligule when present. The great range in length of the corolla to be found in *Crepis* is shown by comparing *C. sibirica* (fig. 13, c) with *C. multicaulis* (fig. 232, d). It may be noted here that the number of ligule teeth in *C. multicaulis* has been reduced from 5 to 4, but this has not been observed in any other species. The reduction in width of the ligule is not always proportional to the reduction in length. In certain species the ligule tends to flare out toward the summit, as shown in *C. aculeata* (fig. 288, h). In certain others it tends to fold up around the anther tube so that it is difficult to determine its width (cf. *C. foetida*, fig. 217, e). The color of the ligules in almost all of the species is some shade of yellow; but there are three pink-flowered species, *C. rubra*, *C. incana*, and *C. incarnata*; also, one white-flowered species, *C. albiflora*, and white-flowered plants of *C. rubra* occur in gardens. Many of the yellow-flowered species also have a reddish stripe on the outer face of the marginal florets, but others lack red color entirely. In *C. bursifolia* the red dorsal stripe is replaced by one of bluish-green. The length of the ligule teeth is very variable between species, though reduction with phylogenetic advancement is the general rule as to length as well as to the prominence of the glandular dorsal crest or anterior knob or lip at the apex of each tooth. In certain species this glandular mass takes on a very distinctive shape which may be helpful in identification. That the relative length of the corolla tube is also variable throughout the genus is seen by again comparing *C. sibirica* with *C. multicaulis* or with *C. achyrophoroides* (fig. 52, d) in both of which the tube is nearly half as long as the whole corolla. But in most of the species the tube is about one-third the length of the corolla. When pubescence is present on the corolla tube it may consist of any one of several types of trichomes or a mixture of two or three kinds. One of the most unusual combinations in *Crepis* is that of *C. achyrophoroides* (fig. 52, d), in which there is a cluster of long, many-celled, acicular trichomes just at the summit of the tube, which is also densely covered with very short, pointed trichomes. The cluster of trichomes at the summit of the tube is frequently present in certain other genera of the Crepidinae, such as *Lactuca*, but is very rare in *Crepis*.

The anther tube and filaments also present a great variety of relative sizes, as is shown by comparing *C. sibirica* (fig. 13, d) with *C. multicaulis* (fig. 232, e) and *C. Zacintha* (fig. 249, m). Similarly with the anther appendages, which are generally longer and broader in the primitive species versus shorter and narrower in the advanced ones; and, as between species, there is considerable variation in their shape.

The style branches also vary widely in length and considerably in width (cf. *C. sibirica* and *C. multicaulis*). But throughout the genus they are semicylindric in shape and are generally attenuate toward the apex. In color the style branches may be dark green, bright yellow, or some intermediate shade.

Achenes.—In this genus the achenes present a remarkable diversity in color, size, and shape, in the details of their apical and basal parts, and in the ribs. But within a species or a subspecies there is relative constancy with respect to all these features. It is for this reason that the identification of the fossil achenes which are illustrated in plate 1 is made with confidence respecting its correctness. In all 3 of these species the achenes are monomorphic, which is true of all the species in sections 1 to 18. In all of these 135 species the achenes are essentially monomorphic, making due allowance, of course, for some differences in shape between the marginal and innermost achenes in a head, since such differences are usually continuous in passing from the marginal ones toward the center of the receptacle. It is only in the advanced sections, 19, 20, 22, 23, 25, and 26, that some or all of the species have dimorphic achenes. Dimorphism in the achenes, therefore, accompanies phylogenetic advancement in this genus. It may well be a form of specialization which somehow aids in the perpetuation of the species. The beak or slender stipe, bearing the pappus at its apex, is another specialized feature of the achenes in many species, since it undoubtedly aids in the distribution of the fruits by the wind. None of the 26 most primitive species (secs. 1–6) has beaked achenes (see fig. C), whereas in all but one of the 27 most advanced species (secs. 25–27) the achenes are beaked, and in the most advanced species of all the beak is extremely fine and delicate (see fig. C). In section 20, also, all of the species have long-beaked achenes, but these species are somewhat more primitive in other characters than those of the most advanced sections (fig. C, lower right). In the rest of the sections most of the species have beakless achenes, but in sections 7, 12, 19, and 24 the most advanced species have developed beaks. In many of the older treatises on *Crepis* the presence or absence of a beak on the achenes was the chief or sole diagnostic character used in classifying under *Barkhausia* or *Crepis*. Since some of the species in such a primitive group as section 8 have more or less definitely beaked achenes, and since one or more such species occur in several intermediate sections, this character obviously cannot be used for such a purpose.

Pappus.—The pappus setae, although simple, barbellulate bristles, also present some useful diagnostic characters. The color ranges from pure white, as in most species, through dusky shades to yellow. The length varies from less than one millimeter in *C. patula* to about one centimeter in some of the most primitive species. The number of series of setae borne on the pappus disk varies from 4 or 5 down to 1. And the thickness of the setae, as indicated by their width at the base, varies from about 20 to about 80 microns. This results in marked differences in degree of rigidity or brittleness as opposed to softness or pliability. It was found by Stebbins (1940) that most *Crepis* species have less coarse pappus setae than are found in *Dubyaea*. But the pappus setae of some of the primitive species of *Crepis* resemble those of *D. chimiliensis*, as illustrated by Stebbins (*op. cit.*, fig. 1, a, b).

Indumentum.—The indumentum of the vegetative parts and involucre may consist of any one of three general types: (1) tomentum of various shades from white to brown and various degrees of thickness; (2) glandless hairs or setae of various lengths and colors from transparent to black; and (3) gland-bearing hairs of similar diversity in size and color. The presence of a certain type or combination of types of indumentum is often fairly constant within a species or subspecies and serves as a valuable additional criterion of classification.

CYTOLOGIC CRITERIA

The chromosomes of related genera.—The earlier reports on chromosome numbers in genera close to *Crepis* have been supplemented by Babcock, Stebbins, and Jenkins (1937), who reported on two species of *Dubyaea*, nine of *Prenanthes*, twenty-five of *Lactuca*, two of *Youngia*, two of *Ixeris*, and one of *Cephalorrhyncus*. These data, added to those reported by others, led to several conclusions, among which the following are pertinent here:

1) The somatic chromosome numbers 16 and 32 occur in *Prenanthes* subg. *Nabalus*; 18 in subg. *Euprenanthes*; 16 in the genus *Dubyaea*; 16, 18, 34, and 36 in the various subgenera of *Lactuca*; 18 in *Cephalorrhyncus*; and 16 or 32 in all the species of *Youngia* thus far reported, except *Y. tenuifolia*, which is a polyploid complex with 15, 20, and 24 chromosomes.

2) The more primitive diploid number in *Dubyaea*, *Prenanthes*, and *Youngia* is probably 16. In *Lactuca* more of the primitive species have this number, and more of the advanced species have 18, but both numbers may have existed since the formation of the genus.

3) The primitive somatic numbers for the Crepidinae are probably 16 and 18, whereas 12, 10, 8, and 6 were derived from them by some process of reduction.

4) The hypothesis that reduction in absolute size of the chromosomes often accompanies evolutionary advancement is borne out by the study of these genera, although certain exceptions were found.

5) The hypothesis that in primitive species most of the chromosomes have median constrictions and the chromosomes of a haploid set are nearly equal in size is borne out by this study, as is the hypothesis that, with advancing evolution, subterminal constrictions are evolved and the chromosomes of a set become unequal in size. It is suggested that the early differentiation of genera in the Crepidinae was accompanied by less structural differentiation of the chromosomes than was the evolution of species groups among the more highly evolved and diversified subgenera.

Thus, the available evidence from closely related genera certainly indicates that similar relations exist between karyotype evolution and phylogenetic advancement to those which exist in *Crepis*. In order to fill the gap between *Crepis* and *Dubyaea*, it is necessary to assume that ancestral species of either genus with 14 somatic chromosomes must have existed but may now be extinct. It is evident, however, that much further botanical exploration in Asia, accompanied by study of the chromosomes, is needed.

The chromosomes of Crepis.—The evidence from *Crepis* on chromosomes and classification and on chromosomes and phylogeny has been reviewed in chapters 1 and 4. In table 2 are listed the 113 species of *Crepis* which have been studied cytologically. They are arranged in approximate phylogenetic sequence, with the section number given in the left-hand column. To the right of each species the somatic chromosome number is given, together with the "chromosome class," that is, whether the species is diploid, dysploid, tetraploid, octoploid, allopolyploid, or euploid. Also, the classification of each species in accordance with the method of reproduction and duration of life is given. A brief examination of this table is sufficient to make clear the general parallelism which exists between phylogenetic advancement, as determined in arranging the sections on a morphological basis, and reduction in chromosome number. The diploid and polyploid species are characterized by sexual reproduction, with the outstanding exception of 9 of the American species in section 15. It should be noted also that the 5 species in section 18 are probably apomictic, but none of them has thus far been studied in living condition.

TABLE 2

CLASSIFICATION OF 113 SPECIES OF CREPIS IN ACCORDANCE WITH SECTION, SOMATIC CHROMOSOME NUMBER, CHROMOSOME CLASS, METHOD OF REPRODUCTION, AND DURATION OF LIFE

Section	Species	Somatic chromosomes		Reproduction	Duration
		Number	Class*		
1	<i>C. sibirica</i>	10	D	sexual	perennial
1	<i>C. geracioides</i>	12	D	sexual	perennial
1	<i>C. viscidula</i>	12	D	sexual	perennial
1	<i>C. paludosa</i>	12	D	sexual	perennial
2	<i>C. kashmirica</i>	12	D	sexual	perennial
3	<i>C. pygmaea</i>	12	D	sexual	perennial
4	<i>C. terglouensis</i>	12	D	sexual	perennial
4	<i>C. Jacquini</i>	12	D	sexual	perennial
4	<i>C. aurea</i>	10	D	sexual	perennial
4	<i>C. hokkaidoensis</i>	8	D	sexual	perennial
4	<i>C. chrysantha</i>	8	D	sexual	perennial
4	<i>C. polytricha</i>	16	T	sexual	perennial
4	<i>C. albiflora</i>	8	D	sexual	perennial
5	<i>C. lapsanoides</i>	12	D	sexual	perennial
5	<i>C. lyrata</i>	12	D	sexual	perennial
5	<i>C. mollis</i>	12	D	sexual	perennial
5	<i>C. willemetoides</i>	12	D	sexual	perennial
5	<i>C. hierosolymitana</i>	12	D	sexual	perennial
5	<i>C. montana</i>	12	D	sexual	perennial
5	<i>C. Mungierii</i>	12	D	sexual	perennial
6	<i>C. pontana</i>	10	D	sexual	perennial
6	<i>C. conyzaeifolia</i>	8	D	sexual	perennial
6	<i>C. blattarioides</i>	8	D	sexual	perennial
7	<i>C. albida</i>	10	D	sexual	perennial
8	<i>C. kilimandscharica</i>	8	D	sexual	perennial
8	<i>C. alpestris</i>	8	D	sexual	perennial
8	<i>C. suffruticosa</i>	8	D	sexual	perennial
8	<i>C. hypochaeridea</i>	8	D	sexual	perennial
8	<i>C. Newii</i>	8	D	sexual	perennial
8	<i>C. scaposa</i>	8	D	sexual	perennial
9	<i>C. tingitana</i>	10	D	sexual	perennial
9	<i>C. leontodontoides</i>	10	D	sexual	perennial
9	<i>C. suberosistris</i>	10	D	sexual	perennial
10	<i>C. ciliata</i>	± 40	O	sexual	biennial
10	<i>C. biennis</i>	± 40	O, A?	sexual	biennial
10	<i>C. pannonica</i>	8	D	sexual	perennial
10	<i>C. latialis</i>	8	D	sexual	perennial
10	<i>C. chondrilloides</i>	8	D	sexual	perennial
10	<i>C. Baldaccii</i>	10	D	sexual	perennial
10	<i>C. Triasii</i>	8	D	sexual	perennial
10	<i>C. Raulini</i>	10	D	sexual	perennial
10	<i>C. oporinoides</i>	8	D	sexual	perennial
10	<i>C. incana</i>	16	T	sexual	perennial
10	<i>C. taygetica</i>	± 40	O?	sexual	perennial
11	<i>C. Schachtii</i>	10	D	sexual	perennial
11	<i>C. bithynica</i>	10	D	sexual	perennial
11	<i>C. oreades</i>	8	D	sexual	perennial
11	<i>C. crocea</i>	16	T, A?	sexual	perennial
11	<i>C. Hookeriana</i>	8	D	sexual	perennial
11	<i>C. Robertioides</i>	8	D	sexual	perennial
12	<i>C. flexuosa</i>	14	D	sexual	perennial
12	<i>C. nana</i>	14	D	sexual	perennial
12	<i>C. elegans</i>	14	D	sexual	perennial
13	<i>C. gymnopus</i>	8	D	sexual	perennial
13	<i>C. praemorsa</i>	8	D	sexual	perennial
13	<i>C. incarnata</i>	8	D	sexual	perennial
14	<i>C. Bungei</i>	8	D	sexual	perennial

* Abbreviations in this column stand for the terms indicated: D, diploid; Dy, dysploid; T, tetraploid; O, octoploid; A, allopolyploid; E, euploid. For definitions of these terms, see p. 35.

TABLE 2—(Continued)

Section	Species	Somatic chromosomes		Reproduction	Duration
		Number	Class*		
14	<i>C. tectorum</i>	8	D	sexual	annual
15	<i>C. monticola</i>	22-88	A, E	apomictic	perennial
15	<i>C. occidentalis</i>	22-88	A, E	apomictic	perennial
15	<i>C. Bakeri</i>	22-55	A, E	apomictic	perennial
15	<i>C. modocensis</i>	22-88	A, E	apomictic	perennial
15	<i>C. pleurocarpa</i>	22-88	A, E	apomictic	perennial
15	<i>C. acuminata</i>	22-88	A, E	apomictic	perennial
15	<i>C. atribarba</i>	22-88	A, E	apomictic	perennial
15	<i>C. intermedia</i>	33-88	A, E	apomictic	perennial
15	<i>C. barbigera</i>	44-88	A, E	apomictic	perennial
15	<i>C. runcinata</i>	22	A	sexual	perennial
19	<i>C. Reuteriana</i>	8	D	sexual	perennial
19	<i>C. palaestina</i>	8	D	sexual	annual
19	<i>C. pulchra</i>	8	D	sexual	annual
19	<i>C. Stojanovi</i>	8	D	sexual	annual
19	<i>C. pterothecoides</i>	8	D	sexual	annual
20	<i>C. alpina</i>	10	D	sexual	annual
20	<i>C. syriaca</i>	10-18	Dy	sexual	annual
20	<i>C. rubra</i>	10	D	sexual	annual
20	<i>C. foetida</i>	10	D	sexual	annual
20	<i>C. eritreënsis</i>	10	D	sexual	annual
20	<i>C. Thomsonii</i>	10	D	sexual	annual
20	<i>C. Kotschyana</i>	8	D	sexual	annual
21	<i>C. multicaulis</i>	10	D	sexual	perennial
22	<i>C. sancta</i>	10	D	sexual	annual
23	<i>C. patula</i>	8	D	sexual	perennial
23	<i>C. Dioscoridis</i>	8	D	sexual	annual
23	<i>C. multiflora</i>	8	D	sexual	annual
23	<i>C. Zacintha</i>	6	D	sexual	annual
24	<i>C. nicaeënsis</i>	8	D	sexual	biennial
24	<i>C. capillaris</i>	6	D	sexual	annual
24	<i>C. parviflora</i>	8	D	sexual	annual
24	<i>C. neglecta</i>	8	D	sexual	annual
24	<i>C. corymbosa</i>	8	D	sexual	annual
24	<i>C. fuliginosa</i>	6	D	sexual	annual
24	<i>C. cretica</i>	8	D	sexual	annual
24	<i>C. apula</i>	8	D	sexual	annual
24	<i>C. Suffreniana</i>	8	D	sexual	annual
25	<i>C. Clausonis</i>	8	D	sexual	perennial
25	<i>C. Fontiana</i>	8	D	sexual	perennial
25	<i>C. Bourgeau</i>	8	D	sexual	perennial
25	<i>C. canariensis</i>	8	D	sexual	perennial
25	<i>C. divaricata</i>	8	D	sexual	per. or bi.
25	<i>C. Noronhaea</i>	8	D	sexual	per. or bi.
25	<i>C. libyca</i>	8	D	sexual	per. or bi.
25	<i>C. vesicaria</i>	8-16	D, E, A?	sexual	per., bi., an.
25	<i>C. Marschallii</i>	8	D	sexual	biennial
26	<i>C. juvenalis</i>	8	D	sexual	annual
26	<i>C. aculeata</i>	8	D	sexual	annual
26	<i>C. amplexifolia</i>	8	D	sexual	annual
26	<i>C. aspera</i>	8	D	sexual	annual
26	<i>C. setosa</i>	8	D	sexual	annual
27	<i>C. bellidifolia</i>	8	D	sexual	perennial
27	<i>C. bursifolia</i>	8	D	sexual	perennial
27	<i>C. nigricans</i>	8	D	sexual	annual
27	<i>C. senecioides</i>	8	D	sexual	annual

* Abbreviations in this column stand for the terms indicated: D, diploid; Dy, dysploid; T, tetraploid; O, octoploid; A, allopolyploid; E, euploid. For definitions of these terms, see p. 35.

GENETIC CRITERIA

Crossability, vigor, and fertility.—The original data on the interspecific hybrids made between 1920 and 1939 are summarized in the list of interspecific combinations at the end of this chapter. These include reports on 195 combinations in which 55 different species were involved. The combinations are arranged in five subdivisions, as follows: *A*. Diploid species in the same section (intraspecific). *B*. Diploid species in different sections (intersectional). *C*. One species polyploid—both in the

TABLE 3
INTERSPECIFIC HYBRIDIZATION IN CREPIS—SUMMARY OF DIPLOID SPECIES

Groups and sections represented in the combinations	Total combinations attempted	Number of combinations giving no hybrids	Number of combinations giving one or more hybrids	Hybrids vigorous: medium to high fertility	Hybrids vigorous: low fertility or sterile	Hybrids weak: low fertility or sterile
Intraspecific combinations*						
I. Secs. 6 and 9	4	1	3		1	2
II. Secs. 10, 19, 20	21	1	20	5	12	3
III. Secs. 24, 25, 26	18	1	17	6	9	2
Totals	43	3	40	11	22	7
Intersectional combinations*						
I. (1, 4, 5, 6, 7, 8, 9)	8	4	4	.	3	1
II. (10, 13, 14, 19, 20)	9	7	2	.		2
III. (23, 24, 25, 26, 27)	34	6	28	..	22	6
I × II	17	10	7	.	2	5
II × III	35	14	21	.	11	10
I × III	24	9	15	.	9	6
Totals	127	50	77	.	47	30

* This grouping of the sections into I, more primitive; II, intermediate; III, more advanced, was used instead of the grouping according to type of root (see chapter 4, table 4) because there were no intraspecific hybrids in sections 1-4, 13, and 21. The totals of intraspecific and intersectional combinations and hybrids are the same with either system of grouping.

same section. *D*. One species polyploid—the two in different sections. *E*. Both species polyploid. In each part the hybrid combinations are arranged by sections and, under each section, in ascending order from more primitive to more advanced species; thus, this facilitates the consultation of data pertaining to any particular section or combination of sections. Concerning hybrid fertility, the original data were, for the most part, expressed in percentages estimated from the proportion of plump achenes produced by the hybrids, usually under open-pollination. But in some instances the degree of fertility was originally recorded as very low, low, medium, or high. When recorded as actual percentages, these were expressed in intervals of 5, except in those of very low fertility, which were recorded as 1, 2, 3, 4, or 5 per cent. For the sake of uniformity the actual percentages found in the original data have been classified as follows: very low, 1-5 per cent; low, 10-25 per cent; medium, 30-65 per cent; high 70-100 per cent.

Parts *A* and *B* have the most significance with reference to interspecific relationships, partly because these data are more numerous, and especially because the expression of hybrid fertility is not complicated by polyploidy. These data are

summarized in table 3. In this representation two features are most striking. Whereas 93 per cent of the intrasectional combinations produced hybrids, and 27.5 per cent of these hybrids were vigorous with medium to high fertility, only 60 per cent of the intersectional combinations produced hybrids, not one of which was both vigorous and of medium or high fertility. Although crossability alone is of dubious value as an index of relationship, yet the difference between these intra- and intersectional crosses is so striking that some degree of significance must be inferred. Moreover, this is strongly supported by the differences in hybrid vigor, as well as in fertility. Only seven, i.e., 17.5 per cent of the forty intrasectional hybrids, as compared with thirty, i.e., 40 per cent of the seventy-seven intersectional hybrids were described as weak and of low fertility or sterile; whereas thirty-three or 82.5 per cent of the intrasectional hybrids were vigorous, and one-third of these were medium or highly fertile, but only forty-seven or 60 per cent of the intersectional hybrids were vigorous, and all were of low fertility or sterile. This evidence certainly indicates that the sections represented by these interspecific hybrids are groups of species which are more closely related to one another than to the members of other sections. To this extent it supports the sectional scheme of classification here adopted.

The data on intersectional crosses in which one parent is polyploid are sufficiently numerous to warrant comparison with the foregoing. Of the twenty combinations attempted, twelve failed to produce hybrids, seven produced one or more vigorous hybrids of low fertility or sterile, and one produced a weak sterile hybrid. These data are in general agreement with the data on diploid intersectional hybrids.

Comparative genetics.—Less work on the comparative genetics of *Crepis* species has been done than was intended at the outset of these investigations. This was due to the early discovery of the possibilities of interspecific hybridization and the long period of time required for assembling the wild species in living condition and for cytologically studying the species and certain hybrids. As a result of the research of several co-workers and students, however, it is possible to present some evidence, based on segregation in hybrid populations, which indicates at least the existence of genic homology between different species.

Plant stature.—Among the twenty-two characters in *Crepis capillaris* which were studied by Collins (1924) were two or more dwarf types which behaved as Mendelian recessives when crossed with plants of normal stature. In *Crepis tectorum* there are two wild dwarf forms in Scandinavia, one of which (fa. *pygmaea* Sjöstr.) is also recessive to tall stature and is inherited according to Mendelian principles.

Leaf "shape," pinnatifid versus dentate margin.—In *C. capillaris*, Collins (*loc. cit.*) reported that pinnate margin is dominant to dentate margin and due to a single gene difference. In a cross between two subspecies of *C. foetida*, Babcock and Cave (1938) found the same relation between pinnatifid and dentate leaves.

Anthocyanin.—The general occurrence of anthocyanin in *Crepis* species was pointed out by Collins (*Science*, 63:52, 1928), who had found large and small amounts of the pigment in the leaves of *C. capillaris* to be inherited as Mendelian characters. He also reported a pure green plant of *C. Dioscoridis* which gave a 3:1 ratio in F_2 when crossed with a normally pigmented plant. It was reported by Babcock and Navashin (1930) that in *C. neglecta* the presence and absence of anthocyanin in the leaves behave as a monohybrid difference. They also reported (*loc. cit.*) that the white-flowered horticultural variety of *C. rubra* behaves as a simple recessive when crossed with typical pink-flowered forms. Babcock and Cave (1938) found anthocyanin leaf spots to be present in some strains of *C. foetida*

and absent in others, whereas it was always absent in *C. eritreënsis* and always present in *C. Thomsonii*. In crosses between the last species and *C. eritreënsis* and between *C. Thomsonii* and certain strains of *C. foetida* lacking these leaf spots, the inheritance was, for the most part, typical of a monohybrid. The same authors (*loc. cit.*) reported that *C. Thomsonii* and *C. eritreënsis* have red ligule teeth on all the florets, whereas in *C. foetida* all except the outer row of florets have yellow teeth. In ten crosses between one or the other of the first two species and seven strains of *C. foetida*, all the F_1 plants had red ligule teeth, and in six F_2 families there was close approximation to the 3:1 ratio; but the other four F_2 families showed extreme deviations from the monohybrid ratio. The following evidence on a similar character in species of section 25 suggests a plausible explanation for these deviations. Jenkins (1939), working with four closely related species of section 25, found that *C. Noronhaea* has a conspicuous red stripe on the dorsal surface of the outer row of ligules and that *C. divaricata* and *C. canariensis* lack this feature; he also noted that it was present in *C. vesicaria taraxacifolia* but absent in *C. vesicaria andryaloides*. In all the crosses in which one parent had the stripe and the other had none and when both parents were homozygous, a ratio of 3:1 (three striped and one nonstriped) occurred in F_2 . Some of the F_1 hybrids from these species crosses, however, failed to show the stripe, even though their progeny segregated as stated above. Jenkins inferred that this was because these F_1 hybrids did not have the proper genic milieu for the development of the stripe; that is, he held that the presence of this character requires not only the dominant gene but also a definite genic background for its expression.

Chlorophyll reduction.—In *C. capillaris*, Collins (1924) discovered at least three different recessive genes for reduction of the chlorophyll; and a recessive gene causing chlorophyll reduction was reported by Babcock and Navashin (1930) in *C. Dioscoridis*.

Erect versus nodding flower buds.—In most species of *Crepis* the heads are erect in all stages of development; but in certain species, viz., *C. neglecta* (sec. 24) and its closest relatives, the branchlets or peduncles bearing young heads are strongly bent downward. This character appears also in the distantly related *C. carbonaria* (sec. 7); and in section 20, seven of the nine species have the young heads always nodding, whereas in *C. alpina* they are always erect; and in *C. foetida* some forms have them nodding and some erect. In crosses between *C. rubra*, with nodding buds, and a form of *C. foetida*, with erect buds, Poole (1932) reported monohybrid inheritance. Similar results were reported by Babcock and Cave (1938) from crosses between *C. eritreënsis* or *C. Thomsonii*, both with nodding buds, and a form of *C. foetida*, with erect buds.

Paleae.—A unique plant of *C. capillaris*, in which every floret was subtended by a bractlike palea, was discovered by Collins (1921, 1924) who reported that it was conditioned by a single recessive gene. In *C. foetida commutata* similar paleae are present on the receptacle, and they have been found in a few forms of *C. foetida rhoeadifolia*; but the latter subspecies usually lacks true paleae, and they have never been found in other forms of *C. foetida*, nor in its close relatives, *C. eritreënsis* and *C. Thomsonii*. Babcock and Cave (1938) reported that from ten crosses involving *C. foetida commutata* as one parent and either *C. Thomsonii*, *C. eritreënsis*, or a form of *C. foetida* lacking paleae as the other parent, all the F_1 plants had paleae, but only one F_2 family gave a 3:1 ratio, whereas six F_2 families gave ratios approximating 15:1 and three produced a trihybrid hybrid ratio close to 51:13. These results show that presence and absence of paleae in *C. foetida* and its two nearest relatives depend on at least three pairs of genes. In this connection it is

significant that in *C. sancta*, which has setuliferous paleae on the receptacle, wild forms with the receptacle naked have been discovered (see Part II, p. 733, m.v. 1).

Self-incompatibility.—Some species of *Crepis*, like *C. tectorum*, *C. pulchra*, *C. scaposa*, *C. multicaulis*, and *C. alpina*, are highly if not completely self-compatible. At least they usually produce selfed seed abundantly under favorable environmental conditions. Some species, like *C. capillaris*, are self-compatible but variable in the quantity of selfed seed produced. Many species, however, produce only small quantities of selfed seed, even under favorable conditions; and some are definitely known to be characterized by self-incompatibility, even though, like other self-incompatible plants, they occasionally produce a few selfed seeds. This is true in *C. foetida rhoeadifolia* and *C. foetida commutata*; but in *C. foetida vulgaris* and in *C. Thomsonii* and *C. eritreënsis* the plants are self-compatible. From preliminary experiments Babcock and Cave (1938) obtained data indicating that *C. Thomsonii* and *C. eritreënsis* differ more from *C. foetida* in the genetic nature of their self-compatibility than the several forms of *C. foetida*, which were used, differ among themselves. Their results also indicated that the genetic basis of self-incompatibility in *C. foetida* was different from any genetic scheme for incompatibility that had previously been reported. M. B. Hughes (1943) made a thorough study of self-incompatibility in *C. foetida rhoeadifolia* from which he concluded that, although a single series of alleles is responsible for the phenomenon, yet, in order to explain aberrant results from reciprocal crosses between two of his seven genotypically different groups, it is necessary to assume that one member of the series of alleles can be either strongly or weakly potent. It is not unlikely that other modifications of the usual genetic scheme for self-incompatibility occur among the many "self-sterile" species of *Crepis*.

Size differences.—Although certain differences in size, such as plant stature, are determined by only one or two genes, almost all of the quantitative differences between those closely related species which have been studied genetically are conditioned by several or many genes, each having a relatively small effect. For example, in hybrids between *C. divaricata* ($n=4$) and *C. vesicaria taraxacifolia* ($n=4$), Jenkins (1939) obtained data on the inheritance of leaf length, length-width ratio in the leaves, diameter of the open flower heads, height of stem, ratio of height to spread of plant, achene length, and length of the beak of the achene. The F_1 hybrids were intermediate and the F_2 exhibited blending inheritance with a range similar to that of the parental extremes. But for most of these characters no recovery of types corresponding to the parents was found, which indicates that the intermediate combinations were mostly able to survive and that a great many genic differences exist between the two species. Furthermore, no new characters appeared in either F_1 or F_2 , which indicates that the gene systems in the two species were essentially the same. Similar generalizations could be made regarding hybrids between all four of the closely related species with which he worked (see p. 17). Babcock and Cave (1938) presented some evidence of multiple factors conditioning quantitative differences in *C. foetida*, *C. eritreënsis*, and *C. Thomsonii*, all with $n=5$. In both of these groups of closely related species the F_1 hybrids were perfectly regular in diakinesis and meiotic metaphase, which indicates that the structure of the chromosomes is closely similar in the several species in each of the two groups. Thus, the genes of one species can be transferred to another species and, since meiosis is regular and the fertility of the hybrids is sufficient to produce numerous progeny, either ordinary Mendelian or multiple gene inheritance ensues according to the nature of the differences observed. From this it may be inferred that the only genetic process of importance in the differentiation within these two groups of

species is gene mutation. In certain others, however, it is clear that other genetic processes have been partly responsible for speciation (see the following section).

Cytogenetics of interspecific hybrids.—The literature in this field up to 1941 has been reviewed (cf. Babcock, 1942), and it is only necessary here to point out certain generalizations and conclusions which have a direct bearing upon interspecific relations in the genus.

Hybrids with high meiotic regularity.—The genetic relations between diploid species, with the same chromosome numbers and nearly identical karyotypes, have been studied in two groups of closely related species, one in section 20 (Babcock and Cave, 1938), the other in section 25 (Jenkins, 1939). In the F_1 hybrids meiosis is just as regular as in the parent species, which indicates that the chromosomes of these species contain no considerable structural differences. In the F_2 generation certain qualitative characters exhibit simple Mendelian ratios, but most of the quantitative differences behave as though conditioned by numerous genes. Hence, it appears that such species differ mainly with respect to their genes and that the decreased fertility which is characteristic of their hybrids is due to such genic differences. This has an important bearing on the causes of evolution in the genus (see p. 24).

Reduced metaphase pairing and interspecific relationship.—The earlier evidence on irregularities in chromosome distribution in the first meiotic division in interspecific hybrids was reviewed by Babcock and Emsweller (1936). Thirteen different hybrid combinations were studied, five by Avery (1930), two by Hollingshead (1930b), three by Babcock and Clausen (1929), one by Müntzing (1934), and two by Emsweller (Babcock and Emsweller, 1936). But three of these hybrids, one by Avery and two by Hollingshead, had as one parent *C. capillaris*, which was found to be highly variable itself in amount of metaphase pairing. For the sake of brevity and simplicity, these data are omitted here. The ten hybrids under consideration are listed below, in ascending order with respect to the degree of primitiveness of the sections represented in the parents.

SECTIONS	SPECIES AND HAPLOID NUMBERS	MEAN NUMBERS OF BIVALENTS
4-9.	<i>aurea</i> 5 × <i>leontodontoides</i> 5	4.7 ± .16
9-14.	<i>leontodontoides</i> 5 × <i>tectorum</i> 4	2.0 ± .26
9-24.	<i>leontodontoides</i> 5 × <i>parviflora</i> 4	2.5 ± .47
9-25.	<i>leontodontoides</i> 5 × <i>Marschallii</i> 4	1.6 ± .22
14-25.	<i>tectorum</i> 4 × <i>vesicaria taraxacifolia</i> 4	2.8 ± .27
23-25.	<i>Dioscoridis</i> 4 × <i>divaricata</i> 4	1.8 ± .23
24-26.	<i>nicæënsis</i> 4 × <i>setosa typica</i> 4	3.9 ± .21
24-26.	<i>nicæënsis</i> 4 × <i>setosa Topaliana</i> 4	3.4 ± .18
26-26.	<i>aculeata</i> 4 × <i>aspera</i> 4	3.5 ± .18
26-27.	<i>aspera</i> 4 × <i>bursifolia</i> 4	2.5 ± .28

It is a generally accepted theory that the pairing of the chromosomes in the meiotic prophase depends upon genic homology. The mean number of bivalents counted at first meiotic metaphase in these hybrids ranges from $1.6 \pm .22$ to $4.7 \pm .16$, and it will be noted that the standard errors are relatively small. This certainly indicates marked differences in the degree of genic homology between the species used in the various crosses.

The first four hybrid combinations, which involve *C. leontodontoides* of section 9, make an instructive series in themselves. The high meiotic regularity found in the hybrids between *C. aurea* and *C. leontodontoides* strongly supports the evidence from comparative morphology, which indicates that *C. leontodontoides* is actually close to the more primitive species, *C. tingitana*, also of section 9. On the other hand, the hybrids between *C. leontodontoides* and three advanced species showed reduced

regularity, forming only about half the number of metaphase pairs that would be possible in a hybrid between a 5-paired and a 4-paired species. It is worth noting also that *C. aurea* and *C. leontodontoides* are indigenous in the same geographic area, although the former is montane and the latter is found in low altitudes. But *C. tectorum*, *C. parviflora*, and *C. Marschallii* are all indigenous in areas widely separated from that of *C. aurea*. For this group of four hybrids the evidence from metaphase pairing is consistent with the evidence from comparative morphology, chromosome number, and geographic distribution of the parent species.

The other six hybrids, all having advanced species for both parents, are consistent, on the whole, with the first four. The first two, however, are probably significantly different with respect to mean number of bivalents, the difference being nearly three times its standard error. Yet the two pairs of species are fairly comparable, *C. tectorum* being somewhat more primitive than *C. Dioscoridis*, and *C. divaricata* certainly more primitive than *C. vesicaria*. In both these hybrids the parent species occur in different areas, but *C. Dioscoridis* and *C. divaricata* are more widely separated geographically than the other two. From the lower meiotic regularity of their hybrid, these two species appear to be less similar genically than *C. tectorum* and *C. vesicaria*. The last two hybrids, *C. aculeata*-*C. aspera* and *C. aspera*-*C. bursifolia*, also have a significant difference in their mean number of bivalents which is consistent with the fact that the parents of the former belong in the same section and occupy the same area, whereas those of the latter are in different sections and occupy different areas. Finally, the hybrids between *C. nicaeensis* and the two subspecies of *C. setosa* are fully as regular in metaphase pairing as the *C. aculeata*-*C. aspera* hybrid, yet the former involve different sections. Although *C. nicaeensis* is more primitive than *C. setosa*, the two species are generally similar morphologically. This is especially clear when *C. setosa typica* is compared with *C. nicaeensis*, and when habit, type of involucre, and size of heads, florets, and fruits are considered. The chromosomes are of the same four types and for the most part similar in size. The two also occur in the same geographic area. Hence, the high meiotic regularity of these hybrids can be interpreted as indicating a certain degree of genic homology in the two species. In this connection it is noteworthy that in the hybrid *C. setosa* \times *C. biennis* (see p. 16) there was no pairing between the chromosomes of the two species. This indicates that there is much less genic similarity between these two species than between *C. nicaeensis* and *C. setosa*.

Structural hybridity and interspecific relationship.—From the study of meiotic irregularities in interspecific hybrids, evidence has been obtained by Müntzing (1934), Sherman (1946), and Tobgy (1943) that the chromosomes of different species contain homologous segments. This research has been summarized briefly in a preceding chapter (pp. 20–21). The hybrids studied by Tobgy and Sherman were between species of the same section, but the one reported by Müntzing was between two species of different sections. This evidence supports the inference, derived from the study of metaphase pairing in other interspecific hybrids, that some degree of homology exists between the chromosomes of different species.

Thus, the available evidence from cytogenetic research on interspecific hybrids supports the conception that all the species of *Crepis* had a common origin and are still more or less similar in genic constitution.

Summary of genetic criteria.—1) Experiments on interspecific hybridization have yielded evidence of considerable significance bearing on the genetic relationships of fifty-five of the species in this genus. In general, the closer their genetic relationship the more easily can species be crossed and the higher is the vigor and fertility of their hybrids. Such experiments provide a valuable criterion for deter-

mining species relationships, and it is highly desirable that further investigations be made in *Crepis*, especially on those sections and species which have not been cultivated and studied cytologically and genetically.

2) From the evidence on intra- and interspecific hybrids in *Crepis* it can be inferred: (1) that similar gene mutations occur in species belonging to widely separated sections; (2) that some closely related species have the same genic milieu but differ in respect to many individual genes; (3) that there is a similar genic background in all the species investigated.

3) Sufficient work has been done on the cytogenetics of interspecific hybrids to demonstrate the significance of metaphase pairing as an indicator of genic homology between the parent species. In this genus there appears to be positive correlation between wide geographic separation and relatively low genic homology. But the available data on *Crepis* hybrids are not adequate for any generalization about phyletic status and meiotic regularity. There should be several series of hybrids all of which involve a single more primitive species as one parent and an ascending series of species for the other parents. So far as possible both parents should occur in the same region. Such a series might be made up from the tropical African species (sec. 8) or by starting again with *C. leontodontoides* and selecting a series from a number of other sections. Similarly, there is ample opportunity in this genus for further significant studies on structural hybridity and karyotype analysis and their bearing on evolution. But the work thus far accomplished proves the importance of reciprocal translocation as a process of speciation in *Crepis*.

4) All of the genetic evidence supports the conception of a monophyletic origin of the genus as a whole.

INTERSPECIFIC HYBRIDIZATION IN CREPIS

In the data that follow, the female parent is given first. Abbreviations stand for the terms indicated, as follows: r, includes reciprocal cross; a, achenes, including parthenocarpic ones; c, developed only to cotyledon stage; w, weak hybrids; v, vigorous hybrids; h, high fertility; m, medium fertility; mh, medium to high; lf, low fertility; vl, very low fertility; s, sterile; vls, very low or sterile.

A. Diploid species in the same section

- Section 6. *conyzaefolia*—*blattarioides*, 2a, 2c, s.
- Section 9. *leontodontoides*—*suberostris*, r, 24a, 9v, s.
leontodontoides—*tingitana*, 17a, 0.
- Section 10. *latialis*—*chondrilloides*, 13a, 13v, lf.
pannonica—*chondrilloides*, 27a, 21v, vls.
pannonica—*latialis*, 33a, 24v, lf.
pannonica—*Triasii*, 61a, 50w, 3v, s†.
- Section 19. *pulehra*—*palaestina*, r, many a, many v, m.
pulehra—*Reuteriana*, 19a, 11v, vl.
- Section 20. *alpina*—*foetida vulgaris*, r, 43a, 2c, 2w, s.
alpina—*rubra*, r, 40a, 10v, vl.
alpina—*syriaca*, r, 34a, 33v, m.
foetida—*Kotschyana*, 3a, 1w, s.
Kotschyana—*rubra*, 2a, 2v, s.
Kotschyana—*syriaca*, 8a, 8v, vls.
alpina—*Kotschyana*, 1a, 1v, s.
Thomsonii—*foetida* ssp., 20 + v, vls-mh.
Thomsonii—*eritreënsis*, r, 12a, 12v, h.
eritreënsis—*foetida* ssp., 30v, vls-mh.
foetida vulgaris—*rubra*, 30a, 26v, lf.
eritreënsis—*Kotschyana*, 25v, s.
foetida—*syriaca*, 7a, 3v, lf.
syriaca—*rubra*, 16a, 0.
Thomsonii—*Kotschyana*, 2v, s.

- Section 24. *capillaris*—*neglecta*, 44a, 1w, s.
corymbosa—*neglecta*, r, 24a, 7v, vl.
neglecta—*fuliginosa*, r, 100a, 19v, vl.
- Section 25. *Noronhaea*—*vesicaria andryaloides*, several v, m.
divaricata—*vesicaria andryaloides*, several v, m.
divaricata—*Noronhaea*, several v, vl.
divaricata—*canariensis*, several v, m.
canariensis—*Noronhaea*, r, several v, vl-lf.
canariensis—*vesicaria* ssp., 16v, s-m.
divaricata—*Clausonis*, 42a, 7c, 6v, mh.
Clausonis—*vesicaria myriocephala*, 11a, 3w + 8v, 1m.
Fontiana—*divaricata*, 9a, 8v, m.
Fontiana—*Noronhaea*, 27a, 24v, mh.
Fontiana—*vesicaria taraxacifolia*, 21a, 17w or v, mh.
- Section 26. *aculeata*—*aspera*, 83a, 35v, m.
aculeata—*juvenalis*, 18a, 12w, s.
amplexifolia—*aspera*, 44a, 17v, vl.
aspera—*setosa*, 1a, 0.

B. Diploid species in different sections

The more primitive parent is listed first; when the less primitive one was the female it is indicated by ♀.

Sections

- 1-6. *sibirica*—*conyzaefolia* ♀, 1a, 0.
1-10. *sibirica*—*pannonica* ♀, 6a, 2c, 1v, s†.
1-25. *paludosa*—*libyca* ♀, 8a, 1w, s.
4-6. *chrysantha*—*conyzaefolia* ♀, 3a, 0.
4-9. *aurea*—*tingitana*, 5a, 3w, s.
4-9. *aurea*—*leontodontoides*, 24a, 9v, lf.
4-14. *aurea*—*tectorum*, 8a, 2c.
4-20. *aurea*—*foetida*, 64a, 0.
4-20. *aurea*—*rubra*, 32a, 0.
4-23. *aurea*—*Dioscoridis*, 14a, 0.
4-24. *aurea*—*capillaris* ♀, 18a, 0.
4-25. *aurea*—*vesicaria taraxacifolia*, 16a, 3w, s.
5-10. *Mungierii*—*oporinoides*, 4a, 0.
5-19. *mollis*—*Reuteriana*, 9a, 0.
5-25. *montana*—*Clausonis* ♀, 14a, 3w or v, s.
5-25. *montana*—*libyca*, 4a, 0.
5-25. *montana*—*vesicaria* ssp. ♀, 23a, 16w, s.
5-25. *Mungierii*—*vesicaria taraxacifolia* ♀, 8a, 7w, s.
5-25. *Mungierii*—*divaricata* ♀, 23a, 2w, 1v, s.
6-7. *conyzaefolia*—*albida*, 1a, 0.
6-8. *blattarioides*—*alpestris*, 22a, 1w, 16v, lf.
6-10. *conyzaefolia*—*pannonica*, 36a, 15v, vl.
6-10. *blattarioides*—*pannonica* ♀, 28a, 11w, s.
6-14. *conyzaefolia*—*Bungei*, 1a, 0.
7-8. *albida*—*alpestris*, 2a, 1v, vl.
7-10. *albida*—*pannonica* ♀, 162a, 34c, 62w, s.
8-9. *alpestris*—*leontodontoides* ♀, 33a, 0.
9-10. *leontodontoides*—*oporinoides*, 1a, 1w, s†.
9-14. *leontodontoides*—*tectorum*, 43a, 17c, 12w, vl.
9-19. *tingitana*—*palacestina* ♀, 12a, 0.
9-19. *tingitana*—*pulchra* ♀, 4a, 0.
9-20. *tingitana*—*foetida* ♀, 19a, 0.
9-20. *leontodontoides*—*foetida*, 43a, 0.
9-20. *tingitana*—*rubra*, 5a, 0.
9-23. *tingitana*—*Dioscoridis*, 13a, 0.
9-23. *leontodontoides*—*Dioscoridis*, 4a, 1c.
9-24. *leontodontoides*—*nicaeensis*, 42a, 0.
9-24. *leontodontoides*—*parviflora*, 24a, 7w, 13v, s.
9-24. *leontodontoides*—*capillaris*, r, 200a, 32w, 89v, s.

Sections

- 9-24. leontodontoides—neglecta, 7a, 0.
 9-25. tingitana—libyca, 5a, 0.
 9-25. leontodontoides—Clausonis, 41a, 8c, 2v, s.
 9-25. tingitana—vesicaria ssp., r, 49a, 0.
 9-25. leontodontoides—vesicaria ssp., r, 47a, 18w, 10v, vls.
 9-26. leontodontoides—aspera, 56a, 9c, 25w, s†.
 9-26. leontodontoides—setosa, 174a, 10c, 3w, 3v, s.
 9-26. suberostris—aculeata ♀, 19a, 7v, s†.
 9-27. leontodontoides—bursifolia, 127a, 21c, 46v, s.
 9-27. leontodontoides—senecioides, 11a, 0.
 10-19. pannonica—pulchra ♀, 36a, 4c, s.
 10-19. latialis—pulchra ♀, 5a, 2c, s.
 10-20. pannonica—rubra, 4a, 0.
 10-20. pannonica—foetida commutata ♀, 6a, 0.
 10-23. pannonica—patula, 33a, 29w, lfs†.
 10-23. pannonica—Dioscoridis, 34a, 9v, s.
 10-23. oporinoides—patula, 11a, 5w, 5v, s.
 10-25. pannonica—divaricata ♀, 69a, 0.
 10-25. pannonica—vesicaria ssp., 10a, 2c, s.
 10-25. oporinoides—canariensis ♀, 57a, 13w, 2v, s.
 10-26. pannonica—aculeata, 9a, 1w, s†.
 13-19. praemorsa—pulchra ♀, 17a, 0.
 13-19. incarnata—pulchra ♀, 16a, 0.
 13-25. incarnata—vesicaria myriocephala ♀, 0.
 13-26. incarnata—setosa, 1a, 0.
 14-19. tectorum—pulchra ♀, 27a, 0.
 14-24. tectorum—nicæensis ♀, 14a, 6c, 3w, 4v, s.
 14-24. tectorum—capillaris ♀, 117a, 88c, 22v, vls.
 14-25. tectorum—Clausonis ♀, 7a, 1c, 1v, s.
 14-25. tectorum—divaricata ♀, 16a, 13v, vl.
 14-25. tectorum—libyca ♀, 3a, 3c, s.
 14-25. tectorum—vesicaria taraxacifolia ♀, 70a, 14c, 39w + v, vls.
 14-26. tectorum—amplexifolia, 5a, 2c, s.
 14-26. tectorum—aspera, r, 20a, 1w, 10v, vls.
 14-26. tectorum—setosa, 30a, 10v, vl.
 14-27. tectorum—bursifolia, r, 22a, 12c, 1w, s.
 19-20. palaestina—rubra, 22a, 0.
 19-20. palaestina—foetida, 7a, 0.
 19-23. palaestina—Dioscoridis, 2a, 0.
 19-23. pulchra—Dioscoridis, 269a, 4c, 1w, s.
 19-25. pulchra—Clausonis, 2a, 0.
 19-25. pulchra—divaricata, 4a, 2c, 2w, s.
 19-25. pulchra—vesicaria myriocephala ♀, many a, 0.
 19-25. palaestina—vesicaria taraxacifolia, r, 22a, 5w, s.
 19-26. pulchra—aculeata, 10a, 0.
 20-24. syriaca—capillaris ♀, 2a, 0.
 20-24. foetida—neglecta ♀, 2a, 0.
 20-25. Kotschyana—libyca, 2a, 1v, vl.
 20-25. Kotschyana—vesicaria taraxacifolia, 15a, 0.
 20-25. rubra—Clausonis ♀, 11a, 0.
 20-25. rubra—vesicaria myriocephala, 32a, 0.
 20-26. rubra—amplexifolia ♀, 5a, 0.
 20-26. rubra—setosa, r, 32a, 2w, s.
 23-24. Dioscoridis typica—neglecta, 1a, 1c.
 23-25. Dioscoridis typica—Clausonis ♀, 21a, 1v, s.
 23-25. Dioscoridis typica—divaricata ♀, 63a, 8c, 1w, s.
 23-25. Dioscoridis typica—vesicaria 2 ssp. ♀, 69a, 8c, 3w, s.
 23-26. Dioscoridis typica—aculeata ♀, 44a, 7c, 18v, vls.
 23-26. Dioscoridis typica—aspera, r, 61a, 6v, vl.
 23-26. Dioscoridis typica—setosa ♀, 6a, 0.
 24-25. capillaris—Clausonis ♀, 12a, 1w, 5v, s.

Sections

- 24-25. *capillaris*—*vesicaria taraxacifolia*, 2a, 1v, vl.
- 24-25. *parviflora*—*Clausonis* ♀, 9a, 3w, 3v, s.
- 24-25. *neglecta*—*vesicaria taraxacifolia* ♀, 29a, 0.
- 24-26. *nicæensis*—*setosa*, 81a, 6c, 2v, vl.
- 24-26. *parviflora*—*setosa* ♀, 1a, 0.
- 24-26. *capillaris*—*aculeata* ♀, 15a, 2c, 2w, 5v, vl.
- 24-26. *capillaris*—*aspera*, 81a, 3w, 24v, vl.
- 24-26. *capillaris*—*setosa*, 16a, 8w, vl.
- 24-27. *capillaris*—*bursifolia*, 29a, 12w, vls.
- 24-27. *parviflora*—*bursifolia*, 10a, 1v, vls.
- 24-27. *neglecta*—*bursifolia*, 6a, 3w, s.
- 24-27. *parviflora*—*senecioides* ♀, 28a, 1w, 8v, s.
- 25-26. *Clausonis*—*aspera*, 12a, 3c, 5v, vl.
- 25-26. *Clausonis*—*setosa*, 3a, 0.
- 25-26. *divaricata*—*amplexifolia*, 5a, 1v, lf.
- 25-26. *divaricata*—*aspera*, 43a, 26w, 5v, vl.
- 25-26. *vesicaria* 3 spp.—*amplexifolia*, 59a, 34v, lf.
- 25-26. *vesicaria* 4 spp.—*aspera*, 124a, 6w, 68v, vl.
- 25-26. *vesicaria* 2 spp.—*setosa*, 18a, 1w, 15v, vls.
- 25-27. *Clausonis*—*bursifolia*, 43a, 6c, 26w, 8v, lf.
- 25-27. *divaricata*—*bursifolia*, 2a, 0.
- 25-27. *vesicaria* 4 spp.—*bursifolia*, 137a, 27c, 82v, lf.
- 25-27. *vesicaria taraxacifolia*—*senecioides* ♀, 17a, 3v, s.
- 26-27. *aculeata*—*bursifolia*, 9a, 7v, vl.
- 26-27. *aspera*—*bursifolia*, 2a, 2v, vl.
- 26-27. *setosa*—*bursifolia* ♀, 1a, 0.

C. One species polyploid—both in the same section

Section 10. *pannonica*—*biennis*, r, many a, 0.

Section 25. *Clausonis*—*vesicaria taraxacifolia* 4n form ♀, 2a, 1c.

canariensis—*vesicaria taraxacifolia* 4n form, r, 21a, 11w, s.

divaricata—*vesicaria taraxacifolia* 4n form, 64a, 11v, lf.

vesicaria taraxacifolia—*vesicaria taraxacifolia* 4n form, 109a, 6w, 50v, lf.

D. One species polyploid—the two in different sections

Sections

- 4-10. *aurea*—*biennis*, 11a, 0.
- 4-11. *chrysanth*—*crocea* ♀, 2a, 0.
- 9-25. *leontodontoides*—*vesicaria taraxacifolia* 4n form, 1a, 1v, s.
- 10-11. *chondrilloides*—*crocea*, 15a, 0.
- 10-13. *biennis*—*incarnata* ♀, 1a, 0.
- 10-19. *biennis*—*palaestina* ♀, 2a, 0.
- 10-19. *biennis*—*pulchra* ♀, 5a, 0.
- 10-20. *biennis*—*rubra*, r, 10a, 1w, 4v, s.
- 10-20. *biennis*—*foetida*, 1a, 1v, s.
- 10-23. *biennis*—*Dioscoridis*, 4a, 0.
- 10-24. *biennis*—*nicæensis*, 45a, 1w, s.
- 10-24. *biennis*—*parviflora* ♀, 37a, 6v, lf.
- 10-24. *biennis*—*capillaris* ♀, 28a, 0.
- 10-24. *biennis*—*neglecta* ♀, 23a, 0.
- 10-25. *biennis*—*vesicaria* 4 spp. ♀, 95a, 0.
- 10-26. *biennis*—*setosa*, 6a, 1 or more v, lf.
- 10-27. *biennis*—*senecioides* ♀, 35a, 0.
- 11-14. *crocea*—*Bungei*, 2a, 2v, lf.
- 11-18. *crocea*—*pulchra* ♀, 35a, 0.
- 23-25. *Dioscoridis*—*vesicaria taraxacifolia* 4n form, 3a, 1c, 1v, s.

E. Both species polyploid

Sections

- 10. *ciliata*—*biennis*, 8a, 1w, 4v, mh.
- 10-25. *biennis*—*vesicaria taraxacifolia* 4n form, 1a, 0.

CHAPTER 4

THE PHYLOGENY OF CREPIS

THE GENERIC RELATIONSHIPS OF CREPIS

EXCEPT FOR one other genus, *Crepis* is the largest in the tribe Cichorieae of the family Compositae, the exception being *Hieracium*. This tribe, which is characterized by the presence of milky juice, the ligulate corollas, and the perfect, usually monomorphic, flowers, is the most natural one in the entire family; but within the tribe the relationships of the genera are very complex and no system exists which has successfully divided it into subtribes. As a first step toward a critical revision of this tribe, Stebbins (unpublished) has prepared a tentative reclassification of the sixty-four genera in the group, based on preliminary studies of comparative morphology, geographic distribution, and chromosome numbers, from which he has kindly permitted me to use such parts as are basic to the present discussion. Stebbins recognizes eight subtribes as follows: (1) Scolyminae, one genus with basic chromosome number $x=5$ or 10 ; (2) Cichorinae, four genera with basic chromosome number $x=9$; (3) Microseridinae, eight genera with basic chromosome numbers $x=9$, 6 , and 5 ; (4) Stephanomerinae, eleven genera with basic chromosome numbers $x=9$, 8 , and 7 ; (5) Dendroseridinae, one genus with basic chromosome number $x=9$ or 18 ; (6) Scorzonerinae, three genera with basic chromosome numbers $x=7$ and 6 ; (7) Leontodontinae, nine genera with basic chromosome numbers chiefly $x=7$, 6 , 5 , and 4 ; (8) Crepidinae, twenty-seven genera with basic chromosome numbers $x=9$ and 8 , except in *Crepis*, which has $x=6$, 5 , 4 , and 3 , and in one exceptional section $x=7$.

Subtribe Crepidinae, according to Stebbins, is a very diverse group, but with close affinities and often complex interrelationships connecting the genera. All the genera seem to have diverged from a common stock, which formed branches or meshes which are still represented by modern genera. The end members of these lines are widely divergent, but the basic genera show close affinities. The genus *Dubyaea* (cf. Stebbins, 1940) is definitely the most primitive genus of the subtribe, and its ancestral stock, which was probably larger and more diverse than the present relic genus, may be taken as the starting point for each of these lines. The five lines, designated by naming the genus nearest to *Dubyaea* first and the most divergent or specialized genus second, are as follows: (1) *Hieracium-Tolpis*, (2) *Launaea-Sonchus*, (3) *Prenanthes-Lactuca*, (4) *Youngia-Ixeris*, (5) *Crepis*.

The *Crepis* line consists of that genus alone, but it contains about as many species as any except perhaps the *Hieracium-Tolpis* line. It shows no direct connections with any species of *Dubyaea*, although the most primitive species of *Crepis* do exhibit resemblances in one character to one species of *Dubyaea* and in other characters to others (cf. pp. 64-65). The *Crepis* line is the only line that does not have the primitive basic chromosome numbers $x=9$ and $x=8$, which are the only ones known in *Dubyaea*. That the *Crepis* line is not derived from any known members of any other line is evident from two facts: (1) none of the primitive species of *Crepis* resembles the primitive members of any other line more than one would expect in members of the same subtribe; (2) the floral anatomy of such species as *Crepis geracioides* shows features more primitive than those known in any other genus of the Crepidinae except *Dubyaea*. On the other hand, *Crepis* resembles the Leontodontinae in habit, floral characteristics, and achenes more closely than does any other genus of the Crepidinae. For this reason the similarity in chromosome

number and karyotype which exists between *Crepis* and the Leontodontinae may be evidence of actual relationship as well as parallel evolution.

It is assumed by Stebbins, therefore, that *Crepis* arose from certain primitive, now extinct, species of *Dubyaea*, which were related fairly closely to the ancestors of the Leontodontinae. The degree of diversity found even in the primitive species of *Crepis* makes it necessary to assume that the different lines and groups now existing in the genus were derived from fairly numerous but interrelated ancestral species. Some of these ancestors must have had 14 and some 16 chromosomes; and the karyotypic differences between all the species of *Crepis* and *Dubyaea* (Babcock, Stebbins, and Jenkins, 1937, p. 194, fig. 2) are so marked that structural differentiation of the chromosomes must have been going on more actively in this ancestral stock than in the progenitors of any other line of the Crepidinae.

Among other lines of the Crepidinae, *Crepis* is most similar to the *Youngia-Ixeris* line. The resemblances between these two lines seem to become less rather than greater when their more primitive species are compared. Therefore, it seems possible that their resemblances are due to the origin of the two lines from similar species of *Dubyaea* and to parallel evolution, rather than to an actual close relationship in recent times. In fact, there are good reasons for considering the *Hieracium-Tolpis* line to be as closely related to *Crepis* as the *Youngia-Ixeris* line. In *Hieracium* are found plants remarkably similar to *Crepis* in habit, involucre, and flowers and sometimes even in their fruits. The terete achenes with equal ribs are characteristic of *Hieracium* and *Tolpis*, but are found in only a few species of the *Youngia-Ixeris* line, chiefly in *Ixeris* subg. *Crepidiastrum* (Nakai) Stebbins (1937a, p. 45) and in the primitive species of *Chondrilla*.

The greatest concentration of both primitive and advanced species of *Crepis* is at present in western Eurasia. This fact, along with the fact that the related Leontodontinae and the *Hieracium-Tolpis* line are predominantly European, was considered by Stebbins to indicate that *Crepis* originated in western Eurasia. This agrees with the hypothesis that the *Dubyaea* ancestors of *Crepis* are now extinct. These ancestors can be assumed to have existed, probably in the early part of the Tertiary period, in western Eurasia, with their relatives, the ancestors of the Leontodontinae and the *Hieracium-Tolpis* and *Launaea-Sonchus* lines. The great orographic and climatic changes which western Eurasia has undergone since early Tertiary times, along with competition with their very numerous and efficient descendants, could easily account for the complete extinction of these ancestors. One living relative, *Dubyaea oligocephala*, occurs in south Central Asia, but in a region which contains many western Eurasian types, such as the genus *Cedrus*. It is recognized by Stebbins, however, that *Crepis* does not show so great a concentration of primitive types in Europe as do the other groups mentioned and that, therefore, some of its ancestors at least may have originated in Asia. The present author's deductions from his detailed study of the distribution of *Crepis* are presented in chapter 5.

THE SECTIONS OF CREPIS AND THEIR INTERRELATIONSHIPS

The twenty-seven sections of *Crepis* recognized in this monograph fall naturally into three main phyletic groups. These groups, however, cannot be distinguished from one another by a sufficient number of constant differences to warrant their establishment as subgenera. They are used here merely as a basis for the discussion of interrelationships. The numerical order of the groups and sections, as well as the species in each section, indicates as nearly as possible in a linear series their relative primitiveness or advancement. Table 4 gives the sections in each group, together with the number of perennial or shorter-lived species in each section.

Group I, with its seven sections and twenty-nine species, considered as a whole, is the most primitive of the three groups on the basis of both morphological and cytological evidence. (1) Morphologically, *Crepis sibirica*, *C. geracioides*, and *C. kash-*

TABLE 4
THE SECTIONS OF CREPIS ARRANGED IN PHYLETIC GROUPS

Section	Number of species	Basic chromosome numbers	Number of perennial species	Biennial or annual species
<i>Group I. The rhizomatous species</i>				
1. Desiphylon.....	4	6, 5	4	..
2. Spathoides	1	6	1	..
3. Omalocline.....	1	6	1	..
4. Brachypodes.....	9	6, 5, 4	9	.
5. Mesomeris.....	8	6	8	.
13. Intybellia.....	3	4	3	.
21. Microcephalum.....	4	5	4	..
<i>Group II. The more primitive taprooted species</i>				
6. Soyeria.....	3	5, 4	3	..
7. Paleya	3	5	3	.
8. Anisoramphus..	26	4	26	.
9. Gephyroides.....	3	5	2	1
10. Berinea	29	5, 4	27	2
11. Macropodes	14	5, 4	14	..
12. Ixeridopsis.....	7	7	7	.
14. Mesophylon	3	4	2	1
15. Psilochaenia	10	11	10	.
16. Lagoseris	5	?	5	.
17. Napiseris.....	1	?	1	.
18. Pyrimachos	5	?	5	..
<i>Group III. The more advanced taprooted species</i>				
19. Phaeacasium	6	4	1	5
20. Hostia.....	9	5, 4		9
22. Pterotheca	1	5		1
23. Zacintha	4	4, 3	1	3
24. Phytodesia	10	4, 3		10
25. Lepidoseris.....	13	4	9*	4*
26. Nemauchenes.....	7	4		7
27. Psammoseris.....	7	4	4	3

* These species are variable with respect to the length of life of the individual plant.

mirica, the most primitive species in the genus, show more resemblance to *Dubyaea*, the most primitive genus in the subtribe Crepidinae, than do any other species of *Crepis*. Although none of the existing species of *Dubyaea* shows close resemblance to any *Crepis* species, yet *C. sibirica* and *C. geracioides* do show resemblance to *D. atropurpurea* and *D. oligocephala* in the lyrate leaves, to *D. oligocephala* in the shape and unequal ribbing of the achenes, and to *D. hispida* in the calyculate,

setose involucre. *C. kashmirica*, on the other hand, shows resemblance to *D. chimiliensis* in habit and leaf shape, to *D. hispida* in involucral characters, to *D. oligocephala* in floral characters, and to *D. atropurpurea* to some extent in the shape and ribbing of the achenes. Furthermore, the large size of the basal leaves, the leafy stem, and the few large heads are common features of all of these species. (2) Karyologically, sections 1–5 are considered the most primitive groups of *Crepis*; this is because these sections are the only ones containing 6-paired species, some of which, *C. kashmirica* and *C. terglouensis*, have the most symmetrical chromosomes of all *Crepis* species. (3) Reduction in length of the life cycle has accompanied morphological reduction and specialization in this genus. It will be noted in table 4 that all the species in Group I and all but four in Group II are perennial, whereas about three-fourths of the species in Group III are biennial or annual. Actually, nearly all of the forty-two species in this last column under Group III are annuals and many of these are precocious and ephemeral.

. Although the most primitive species of *Crepis* have a rhizome instead of a true root, yet several taprooted species in sections 6–10, with 5 and 4 pairs of chromosomes, are also very primitive types. There is considerable evidence in *Crepis*, especially the obvious close relationship between sections 4, 9, and 14 and between sections 13 and 19, discussed below, that the taprooted type was derived from the rhizomatous type. At least one species of *Dubyaea* [cf. *D. tsarangensis* (W. W. Smith) Stebbins] has strong, fleshy surface roots instead of a true taproot; and similar fleshy, fibrous roots are found in *Prenanthes sinensis* (Hemsl.) Stebbins. Some species of *Youngia* and *Ixeris* are also characterized by having a rhizome. It seems justifiable, therefore, to assume that the ancestors of *Crepis* as well as the existing species of *Dubyaea* were rhizomatous. Such an assumption is consistent with the conception that *Dubyaea* had its early development in a temperate climate at low elevations and under moist conditions, all of which conditions probably existed in Central Asia in late Oligocene and early Miocene time (see Appendix 1, p. 157). Unfortunately, observations on the seedling root systems of the primitive rhizomatous species have not been reported. If the young seedlings of such species also have root systems resembling those of taprooted species, invocation of the biogenetic law would seem fully warranted. In other words, the taproot may have been characteristic of the more remote ancestors of *Crepis*, whereas the rhizome evolved in the immediate ancestors of *Crepis* through mutations favoring adaptation to a more moist environment. Furthermore, the occurrence of the taproot in the more advanced species of the genus can be explained as the result of mutations favoring persistence of the seedling root and suppression of the rhizome accompanying gradual adaptation to a more xeric environment.

With reference to the chromosomes, it may be assumed that, in the *Dubyaea*-like ancestors of *Crepis*, reduction in number from 8 to 7, 6, or 5 had already occurred.

The seven sections in Group I fall into two subgroups on the basis of relative degree of primitiveness. Sections 1–5 are all primitive morphologically, whereas sections 13 and 21 are more advanced. On the basis of degree of resemblance, however, sections 1, Desiphylon, and 5, Mesomeris, are closer to each other than to the other five. The more primitive species in section 5, like all those in section 1, have a strong horizontal or oblique rhizome and tall leafy stems; but in the more advanced species of section 5 the rhizome is praemorse, as in section 4, and the stems shorter, more slender, and with smaller leaves. Types of involucre, flowers, and fruits are in general agreement with this statement.

Crepis kashmirica (sec. 2) has one of the two most primitive karyotypes in the genus, the other being that of *C. terglouensis*. Except that the leaves are not at all

lyrate and the florets are somewhat smaller than one might expect in such a primitive species, *C. kashmirica* could pass as a member of section 1. It has the most prominently ribbed achenes of all the species in the genus, this being a characteristic of other primitive species, such as *C. sibirica*, *C. pygmaea*, *C. terglouensis*, and *C. pontana*. It is also noteworthy that in *C. kashmirica* the marginal achenes are sometimes parthenocarpic and that these seedless fruits strongly resemble typical achenes of *Youngia* species in shape and ribbing. Normal marginal achenes of *C. kashmirica* retain this resemblance to some extent. Hence, this species appears to be a primitive relic in which the florets have become considerably reduced in size. This phenomenon of marked reduction in one or two organs or parts in otherwise primitive endemic species occurs elsewhere in the genus, most notably in *C. patula*.

In the single species in section 3, *Crepis pygmaea*, the plant spreads by stolons, often developing long subterranean stems. The flowering stems and leaves are much reduced. Evidently this species has become especially adapted to the peculiar conditions obtaining on the loose, gravelly soils of steep mountain slopes. At the same time, the strongly ribbed achenes are very primitive, especially in subsp. *anachoretica*, in which the ribs are alternately wide and narrow. The species exhibits strong resemblances in the leaves, in both adult and seedling stages, as well as in its achenes, to *Youngia depressa* (Hook. f. et Thoms.) Bab. et Stebbins (1936), which is the most primitive species in that genus. In its tufted habit, spatulate leaves, and short, thick, strongly ribbed achenes, *C. pygmaea* also shows marked resemblance to *Soroseris umbrella* (Franch.) Stebbins (1940), which is considered by Stebbins as forming a connecting link between *Soroseris*, *Youngia*, and *Dubyaea*. These definite indications of genetic relationship between one of the most primitive *Crepis* species and the most primitive species in both *Soroseris* and *Youngia*, and between all three of these genera and *Dubyaea*, is of special importance in connection with the problem of the region of origin and early development of *Crepis*.

Brachypodes, section 4, must also be considered as a primordial derivative from the original *Crepis* stock. The most primitive species, *C. terglouensis*, has the tufted habit and short, thick, strongly ribbed achenes which are common to *C. pygmaea* and its relatives in *Youngia* and *Soroseris*; but its leaves are lanceolate and pinatifid and the involucre is definitely more primitive than in *C. pygmaea*. The 6 pairs of chromosomes also comprise a more primitive karyotype than that of *C. pygmaea*. It is especially noteworthy that in all the species of this section the stems are scapiform in contrast with the strongly branched, leafy stem characterizing the species in the other most primitive sections (in *C. pygmaea* the stem, although short, is usually branched). Thus, it appears that this section arose from a different *Dubyaea* type from the one that produced sections 1, 2, 3, and 5. It is highly probable that this *Dubyaea* type had already become adapted to alpine conditions.

Intybellia (sec. 13) and Microcephalum (sec. 21) are comprised of more advanced species; but in each the praemorse rhizome indicates a phylogenetic connection with the more primitive sections of this group. Since in each species the stem is more or less branched, forming a cymose or racemose inflorescence, these sections were probably derived from the 1-5 line rather than the 4 line.

The relationships of these sections to each other and to the other sections of the genus are shown in figures 3 and 4. The distribution of all the sections will be discussed in the following chapter.

Group II, containing twelve sections and 110 species, is much the largest of the three groups. For the first six sections (6-11) and another (14) the phylogenetic connections appear to be very certain. For the rest (secs. 12 and 15-18) they are more hypothetical but for the most part, it is believed, fairly dependable.

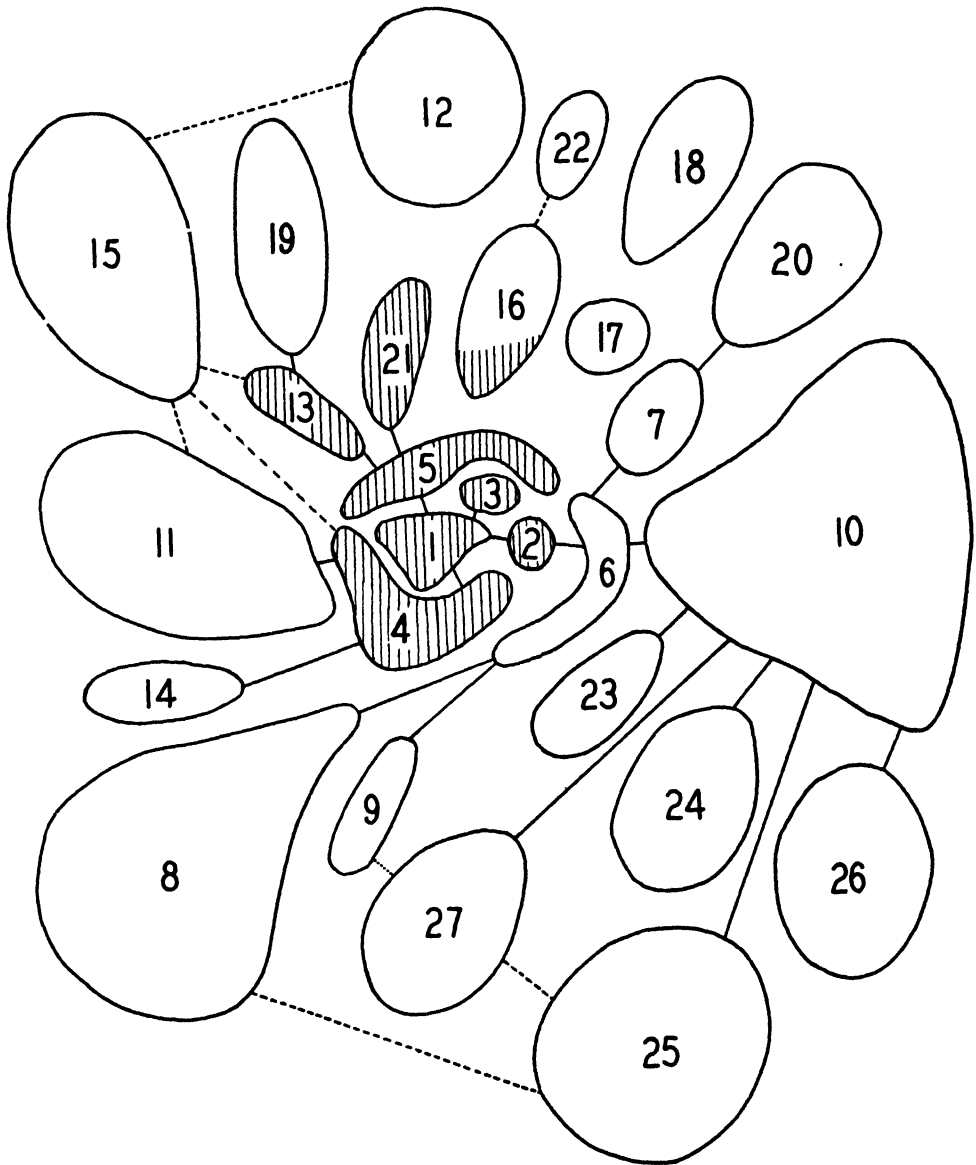


Fig. 3. Cross-sectional chart showing present-day interrelationships of the sections of *Crepis*. Shaded sections contain the rhizomatous species. The lines joining certain sections indicate assumed earlier connections, the solid ones showing more definite relationships than the broken ones. The phylogenetic relationships between the sections are not and cannot be adequately shown in this diagram.

Section 6 contains the most primitive 5-paired species in the genus (except *C. sibirica*), viz., *C. pontana*, which, except for the deep-rooted habit and the non-lyrate leaves, could pass as a member of section 1. The leaves of *C. pontana*, like those of the other species in this section, resemble the leaves of *C. kashmirica* more than those of any other primitive species. Although the species of section 6 are characterized by a deeply penetrating taproot; yet in one of them (*C. blattarioides*) the upper part of the root is often thick, sometimes horizontal, and always strongly

fibrous. These peculiarities certainly suggest a derivation from a rhizomatous type. Thus, it seems highly probable that section 6 was derived from the same line that produced *C. kashmirica*. The most primitive 4-paired species in the genus are *C. conyzaefolia* and *C. blattarioides*. Morphologically they are fairly close to *C. pontana*, though more reduced, and the karyotype of *C. conyzaefolia* is somewhat similar to that of *C. pontana*. Both *C. pontana* and *C. blattarioides* are relic species of the Alps, in contrast with *C. conyzaefolia*, which extends from the Pyrenees to the Altai.

Sections 7 and 9 are small but very interesting groups believed to have been derived from the 2-6 line (fig. 4). Each contains one more primitive species, *C. albida* of section 7 and *C. tingitana* of section 9. In both sections, also, the most primitive species occurs in both Spain and Morocco. But there the similarity ceases, since the distribution of the other two species is different in the two sections, and morphologically *C. albida* and *C. tingitana* are very different, although both have $n = 5$ chromosomes. *C. albida* exhibits definite affinity with *C. alpina* of section 20 but is a much more primitive species, whereas *C. tingitana* shows some resemblance in type of root and achenes to section 8. It should be noted that *C. leontodontoides*, also of section 9, provides further important evidence for the derivation of the taproot type from the rhizome type in *Crepis*. With respect to root, this species is actually variable, some plants being deep-rooted and some shallow-rooted. Furthermore, F_1 hybrids between *C. leontodontoides* and *C. aurea* of section 4 were found by Avery (1930) to exhibit almost perfect premeiotic chromosome pairing, which certainly indicates close genetic relationship between the two species. Thus, *Gephyroides* (little bridge) is a very appropriate name for section 9.

Sections 8 and 10, the two largest sections in the genus, were apparently derived from section 6 or from the 2-6 line. The connection of section 8 with section 6 is obviously through *C. alpestris* of section 8 and *C. conyzaefolia* of section 6, since these two species are morphologically certainly fairly close. Furthermore, the karyotype of *C. alpestris* of section 8 is similar to that of *C. blattarioides* of section 6. Although the connection between section 10 and section 6 is less obvious, yet it can hardly be less certain when all the evidence is considered. The four most primitive species in section 10, on the basis of the large size of the plant and all its parts, are little known endemics from the mountains of eastern Turkestan, western Persia, and the eastern end of the Caucasus region in southern Daghestan. Their chromosomes have not been seen, but they probably have either 5 or 4 pairs. Fairly close to them morphologically are the three diploid species, *C. pannonica*, *C. latialis*, and *C. chondrilloides*, each of which has $n = 4$ chromosomes and a karyotype very similar to that of *C. conyzaefolia*. At the same time, the most primitive species in another subgroup of section 10, *C. Baldaccii*, has a karyotype resembling that of *C. pontana*, the most primitive species of section 6. Furthermore, the evidence from geographic distribution in both section 10 and section 8 is wholly consistent with the assumption that these two large sections were derived from the 2-6 line.

Section 11 contains fourteen species with mostly low scapiform stems and dentate or pinnatifid basal leaves. Except for the deeply penetrating taproot, these plants show more resemblance to the species of section 4 than to any other section; and there are some indications that they have been derived from rhizomatous ancestors. Thus, in *C. bithynica* and *C. Robertioides* numerous fleshy fibers are sometimes present just below the caudex, a feature characteristic of a praemorse rhizome; and

Fig. 4. Phylogenetic relations of the sections of *Crepis*. Large numerals are section numbers and small numerals are basic chromosome numbers. Shaded sections contain the rhizomatous species. Sizes of the circles are roughly proportional to the number of species in the sections. Connections shown by broken or dotted lines are less definitely indicated by the morphological evidence than those shown by solid lines.

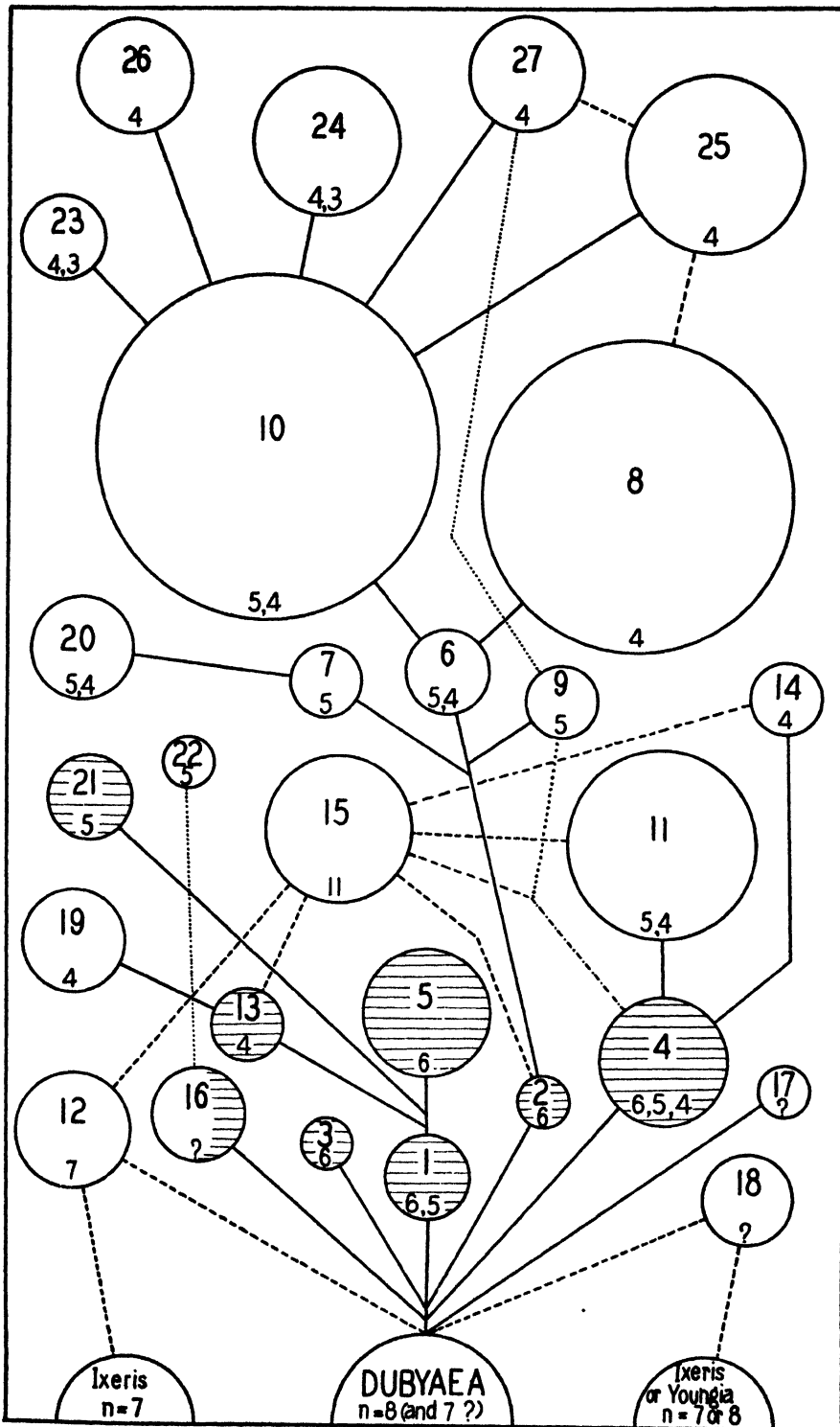


Fig. 4. (For explanation of figure, see bottom of facing page.)

in *C. crocea* and *C. Faureliana* the caudex is swollen and the taproot very slender. Furthermore, the involucre and achenes of *C. Schachtii*, the most primitive species of section 11, resemble those of *C. Jaquini*, *C. aurea*, and *C. chrysantha* of section 4. The geographic distributions of the two sections are consistent with the assumption that they represent the same phylogenetic line.

Mesophyllion, section 14, consists of three closely related species, the well-known *C. Bungei* and *C. tectorum*, and the very little-known *C. ircutensis*. *C. Bungei*, a perennial species, grows in southern Siberia, where it forms mats in swamps or moist meadows and on riverbanks. This mat-forming habit is made possible by the branching of the very slender roots and by the forming of adventitious buds. Morphologically, *C. Bungei* strongly resembles *C. chrysantha*, which has a praemorse rhizome, but does not form mats. *C. Bungei* also has a several-headed stem, and the involucre are more reduced and somewhat specialized. But, aside from these differences, the resemblances are truly striking in the leaves, in the involucre bracts, in the florets, especially in the purplish-brown achenes, in the white, 2-seriate pappus with unequal, persistent setae, and even in the areolate receptacle with short, fine cilia scattered on the interspaces, a rather unusual feature in *Crepis* (cf. figs. 28 and 164). Furthermore, the karyotypes of *C. Bungei* and *C. chrysantha* are almost identical. Thus, it appears certain that section 14 was derived directly from *C. chrysantha* of section 4 and that we find here further evidence of the derivation of the taproot type from the rhizome type. The similarity in morphology extends to *C. ircutensis* and *C. tectorum* and the latter's karyotype is also closely similar. Hence, its inclusion in this section, even though it has become a widespread, aggressive annual, is fully justified. Mesophyllion is certainly an intermediate group, as the name implies, with definite primitive connections and certain advanced aspects (cf. fig. 4).

Considering the other five sections in Group II, we find that each one presents its own peculiar problem. Since none of them throws any light on the main problem of phylogeny within the genus as a whole, they will be discussed very briefly here, leaving consideration of the detailed evidence for the individual sections. Taking them up in numerical order, the origin of *Ixeridopsis* (sec. 12), the only section with the haploid number 7, can be most reasonably explained through intergeneric hybridization between certain now-extinct *Crepis* species and such 7-paired *Ixeris* species as *I. alpicola*, which exhibits considerable resemblance to *Crepis elegans*. This hypothetical origin of section 12 was first suggested by Babcock, Stebbins, and Jenkins (1937), who pointed out that this hypothesis is more satisfactory from the point of view of the present geographic distribution of the two genera than the hypothesis that section 12 represents the link through which *Ixeris* has been derived from *Crepis* or vice versa (see fig. 4, lower left). The evidence in support of this hypothesis is discussed under section 12 (Part II, p. 528).

Psilochaenia, section 15, comprises all the indigenous American species except *C. nana* and *C. flexuosa*. Like *Ixeridopsis*, this section is unique with respect to chromosome numbers, all the species in the section being polyploids, with the base number $x=11$. The probable origin of all the 22-chromosome American species through hybridization of 7- and 4-paired or 6- and 5-paired diploid Asiatic species, followed by amphidiploidy and migration of the new species into North America, where further hybridization, together with polyploidy and apomixis occurred, has been fully discussed by Babcock and Stebbins (1938). The evidence is summarized under section 15 (Part II, p. 572). It should be noted here that sufficient morphological resemblance has been found between some of these American species and certain species of sections 2, 4, 11, 12, 13, and 14 to warrant the assumption that

the diploid ancestors of section 15 belonged to or figured in the ancestry of all those sections. The assumed relationship of section 15 to the other sections mentioned is represented in figure 4 by broken lines.

The remaining three sections in Group II are the only ones in the genus which have not been brought under cultivation and examined cytologically. Each is a unique group in certain aspects. *Lagoseris* (sec. 16) contains five perennial species, all with setiform paleae on the receptacle. Two of these species are endemic in western Persia, two in eastern Asia Minor, and one in Crimea. The only other *Crepis* species with such paleae is *C. sancta* (sec. 22, Group III), a widespread, polymorphic annual. This species, although greatly reduced and specialized, particularly in its desert forms, may have been derived from the same line that gave rise to the five species in section 16. At least one of these species, *C. purpurea*, is rhizomatous; and another one, *C. frigida*, spreads by stolons. Hence, it is assumed that this section arose from the same group of closely related *Dubyaea* species that produced sections 1–5. From the general appearance of the plants it seems likely that most of the *Lagoseris* species have either 5 or 4 pairs of chromosomes, although *C. conneza*, judging from the large size of its pollen grains, might have 6 pairs.

Crepis napifera is an anomalous species the features and relationships of which are considered in detail under section 17. The evidence at present available indicates that it originated from a primitive stock of *Dubyaea* which was probably the ancestral stock of both *Crepis* and *Youngia*.

The last section in Group II, *Pyramachos*, contains five species which are distinct from all other *Crepis* species, as well as from *Ixeris* and *Youngia*, in the nearly leafless caudex and the peculiarity of having the leaves on the lower part of the stem represented by small, scalelike organs. The small, few-flowered heads and the achenes, although generally *Crepis*-like, show some resemblances to those of both *Youngia* and *Ixeris*. But, for reasons stated in the discussion of this section (Part II, p. 634), it is concluded that these species must be included in *Crepis*, although they show definite affinity with *Youngia*. It is possible that they originated from a common ancestral stock or that, like section 12, they resulted from intergeneric hybridization between *Crepis* and both *Youngia* and *Ixeris* at a time when these genera were not strongly differentiated from one another. The latter hypothesis is indicated in figure 4, lower right.

Group III contains eight sections and fifty-seven species. More than half of these species are annuals and several are aggressive, with wide distributions. Along with this marked evidence of advancement in evolution has gone more or less reduction in size of the plant and all its parts; also, a certain degree of parallelism in karyotype modification has taken place. That these progressive changes have not been confined to one or two lines but are general within the genus is evident from the fact that these advanced sections are so numerous and that they are so distinct from one another. This is another argument supporting the conception of the close genetic relationships within the genus as a whole.

Phaeasium, section 19, with six species, has been mentioned (p. 43) as providing evidence that taprooted groups have originated from rhizomatous ancestors. This evidence is found in the one perennial species of this section, *C. Reuteriana*, which is polymorphic. In both subspecies the rootlike, subterranean stem is strongly woody and elongated, sometimes horizontally; at the same time it is usually swollen at the top, and the upper part always bears many strong lateral roots resembling the fibers produced on true rhizomes. This peculiar structure of the underground part of the plant strongly suggests the derivation of this species from a rhizomatous ancestor. It is significant that the karyotypes of the species in this section and

in section 13 are indistinguishable. This indication of relationship between the two sections is supported by a certain amount of morphological resemblance, especially in the involucre, flowers, and fruits, even though they are very distinct in habit, leaves, and pappus, as well as in the pubescence on the corolla tube, which again is intermediate in *C. Reuteriana*. The close relationship of *C. Reuteriana* to the other species in this section is obvious (cf. Part II, p. 649 and figs. 199–201).

Hostia, section 20, is certainly related to Paleya, section 7, although all nine species of Hostia are annuals. This relationship is shown by the peculiar outer involucre bracts in all three species of Paleya and in *C. alpina* and *C. syriaca*, the two most primitive species of Hostia; it is also shown by similarities in the leaves and especially in the achenes. These are long-attenuate in *C. albida* and beaked in the other two species of Paleya, whereas at least the inner ones are more finely beaked in all the species of Hostia. *C. albida* has $n=5$ chromosomes, as have all the species of Hostia except *C. Kotschyana*, a derived species; the karyotypes of six 5-paired species of Hostia and the karyotype of *C. albida* are also similar.

Pterotheca, section 22, with its one species, *C. sancta*, is karyotypically very similar to section 21 of Group I; but on morphological grounds it is much closer to Lago-seris (sec. 16, Group II), concerning which nothing is known cytologically. These morphological resemblances in habit, leaves, involucre, flowers, fruits, and the receptacular paleae extend in some parts to numerous fine details. Here, then, is the most obvious relationship of *C. sancta*; and its geographic distribution fits perfectly with the conception that this aggressive, widespread annual was derived from one of the endemic perennials in section 16 or a similar but now-extinct species. This is indicated by the dotted line connecting 22 and 16 in figure 4. It should be noted, however, that not only does considerable morphological resemblance exist between *C. sancta* and *C. multicaulis* of section 21 but that the karyotypes of the two species are very similar. On this basis it might appear that section 21 was also derived from section 16. But the other three species of section 21 show closer resemblance to section 5 than to section 16, so that the derivation of section 21 from the 1–5 line seems more probable (see fig. 4).

Zacintha, section 23, like section 14, has one primitive species and one very advanced species, the other two being intermediate. The first, *Crepis patula*, an Algerian endemic, is definitely primitive in the woody, modified-rhizome type of root, in the lyrate basal leaves, in the few medium-large heads, in the large florets, and in the large, many-ribbed achenes. In these respects it resembles *C. Strausii* and *C. Raulini* of section 10 more than any other species. This resemblance, however, is not particularly close, and it is probable that the immediate ancestor of *C. patula* is now extinct. As in *C. Reuteriana*, the peculiar root of *C. patula* certainly indicates a connection with the primary *Crepis* line. This species is remarkable in that, along with its primitive characteristics, it has become highly specialized in one respect and extremely reduced in another. The specialization referred to, that of the tendency of the involucre to remain closed in fruiting heads and to become indurate and, in the advanced species, more or less thickened, is also characteristic of the section as a whole. This tendency is extremely marked in *C. patula* (hence the name given by Poiret to the genus founded on it). In the most advanced member of the group, *C. Zacintha*, this tendency also holds, as it does in *C. Dioscoridis*, but to a less extent, and in *C. multiflora*, to a still less extent. The reduction in *C. patula* (mentioned above) is in the extremely short pappus, it being less than 0.5 mm long. In this peculiarity *C. patula* is unique, not only to the section alone, but in the whole genus. The smaller size of the 4 chromosomes of *C. patula*, as compared with those of *C. Dioscoridis* and *C. multiflora*, also suggests that, although this is a fairly

primitive species morphologically, yet it has actually undergone a number of reduction processes. Much greater reduction and specialization, however, is found in the 3-paired *C. Zacantha* which also has a fairly short pappus, only 1.5 mm long. This is a widespread annual of the Mediterranean region. *C. Dioscoridis* is indigenous in Greece, and *C. multiflora*, in the Aegean region. The significance of these distributions in relation to that of *C. patula* is worthy of consideration (see Part II, p. 742).

Phytodesia, section 24, contains ten species, the most primitive being the usually biennial species, *C. nicaeensis*. This species exhibits so many resemblances to *C. biennis* of section 10 that the two are often misidentified. Yet *C. nicaeensis* is definitely more reduced in the small outer involueral bracts, smaller florets, and smaller, 10-ribbed achenes. At the same time, the resemblance between the two is so marked as to warrant the assumption that the 4-paired *C. nicaeensis* was derived from a 5-paired ancestor of *C. biennis*, a polyploid species. Also, the similarities are sufficient throughout all ten species to support the derivation of this section from section 10, since they are all species of the Mediterranean region in the widest sense.

Lepidoseris, section 25, contains thirteen species, most of which are known to have $n = 4$ chromosomes, and all are of the Mediterranean region, including the Madeira and Canary archipelagoes and the Caspian region. The more primitive species, like *C. spathulata* and *C. canariensis*, with their strong perennial root, large leaves, leafy stem, and very shortly beaked achenes, show some resemblance to the primitive members of section 10; and it is not unreasonable to assume that they were derived from those or similar species. Although some of the species in the preceding section have shortly beaked achenes, this appears to be a parallel development in a similar but different line also derived from section 10. At the same time, it should be noted that some of the north African members of section 25 exhibit more or less resemblance to members of section 8. This is especially notable in the little-known *C. Claryi* of the Sahara Atlas in southern Algeria. In its habit, leaf shape, involucre, flowers, and fruits, this species shows more or less resemblance to *C. congoensis* or *C. ugandensis*. There is also marked similarity between the karyotype in section 25 and the karyotype of several species in section 8. There is nothing surprising in this, since both sections 8 and 10 are believed to have descended from species such as those now existing in section 6. This possibility that section 25 originated partly from section 10 and partly from section 8 or from common ancestors is indicated in figure 4.

Nemauchenis, section 26, consists of seven species, all of which are highly specialized, short-lived annuals, occurring mostly in Mediterranean littoral regions. Like the species of section 25, these plants show sufficient resemblance in habit, leaves, flowers, and fruits to species of section 10 to warrant the assumption that they were derived from them or from common ancestors. The section as a whole is characterized by peculiar modified marginal achenes; and those of *C. aspera* are sufficiently similar to those of *C. Dioscoridis* of section 23 to have caused de Candolle to place these species together in the genus *Endoptera*; but the two are so different in most respects that such a grouping is not at all justified. The similarity of the marginal achenes of *C. Dioscoridis* to those of *C. aspera* must represent parallel evolution.

Psammoseris, section 27, like many other sections of *Crepis*, contains perennial and annual species. But the four perennial species are all greatly reduced, especially the involucre and fruits; and the three annual species, all of which occur on the north African littoral, are the most extremely reduced and specialized species in the genus. Two of the perennials, *C. Rueppellii* of northeastern Africa, and *C. Forskalii* of an adjacent region in Arabia, are very similar and quite distinct

from the other perennials of this section. In gross morphology they are sufficiently like the more primitive species of section 25 to suggest that they also were derived from section 10 or from common ancestors. The other two perennials, *C. bellidifolia* and *C. bursifolia*, both of the north Mediterranean littoral, are very distinct from each other. *C. bellidifolia* is the more primitive of these two, and it is noteworthy that it also shows some resemblance to *C. leontodontoides* of section 9. This is the reason for the dotted line connecting these two sections in figure 4. It is difficult to say more about the three annual species than that they may have developed from members of section 10 or section 25 or similar now-extinct species.

SUMMARY

1) The Crepidinae is one of the eight subtribes of the tribe Cichorieae of the Compositae. In the Crepidinae, five phyletic lines, streams, or branches are recognized as having been derived from the primitive genus *Dubyaea*. One of these branches is the genus *Crepis*, and the one most similar to *Crepis* is the *Youngia-Ixeris* line, which must have had an Asiatic origin. But the *Hieracium-Tolpis* line may be considered just as closely related to *Crepis*. Furthermore, the most primitive species of *Hieracium* now exist in Europe, which might seem to indicate a European center of origin for this mesh. Nevertheless, the present author believes that the whole subtribe Crepidinae had its origin in Asia.

2) The twenty-seven sections of *Crepis* fall naturally into three groups: I, the rhizomatous species; II, the more primitive taprooted species; and III, the more advanced taprooted species.

3) Evidence has been presented showing that, in sections 6, 9, 11, 14, 16, 19, and 23, taprooted species have developed from rhizomatous ancestors. This evidence supports the assumption that all the taprooted species of *Crepis* developed from rhizomatous ancestors.

4) On the basis of this and other morphological evidence, together with evidence from interspecific hybrids and comparative karyology, it is assumed that sections 6-10, 20, and 23-27 represent a single phylogenetic line, with some cross connections; also that twenty-four of the twenty-seven sections represent a common stream of development from *Dubyaea*-like ancestors, along with many complex interrelationships.

5) The other three sections are also assumed to have arisen from the same *Dubyaea* ancestors as the rest of the genus. Section 17 (*C. napifera*) is an anomalous species the closest affinity of which appears to be with *Crepis*. Except for this species and the twelve species in sections 12 and 18, which are assumed to have originated through hybridization between *Crepis* or *Crepis*-like *Dubyaea* species and primitive *Ixeris*-like or *Youngia*-like *Dubyaea* species, the genus as a whole must be considered as monophyletic.

CHAPTER 5

THE GEOGRAPHIC DISTRIBUTION OF CREPIS

THE REGIONAL DISTRIBUTION OF CREPIS SPECIES

THE GEOGRAPHIC DISTRIBUTION of the individual species is discussed in connection with the interrelations of the species within each section in the taxonomic part of the monograph, and distributional maps are provided for most of the sections. The present discussion deals with the general aspects of distribution within the genus and of the genus as a whole in comparison with the distributions of related genera, the main purpose of this being to determine, if possible, the region of origin and early development of the genus. That a single center of origin for *Crepis* is to be assumed is certainly warranted by the morphological, cytological, and genetical evidence reviewed in preceding chapters. This evidence led to the definite conclusion that the genus is monophyletic. At the same time, the phylogenetic relations within the genus are very complex, and a careful study of geographic distribution should throw further light on these relations as well as on those between this genus and nearly related genera. Since the species have been arranged in three main phylogenetic groups, primitive, intermediate, and advanced, it will be of special interest to ascertain whether there is evidence of agreement with the general principle of Matthew (1915, p. 180) that at any one time in a large group of organisms showing close phylogenetic relations the most conservative will be found farthest from the center of origin and the most advanced, nearest to the center of origin. The data on distribution of the species are summarized by sections for each of the three large groups of sections in tables 5, 6, and 7.

Group I (table 5) includes the 30 rhizomatous species, of which 14 have a European distribution and 12 an Asiatic distribution; the other 4 occur in Asia Minor, the Caucasus region, and western Persia. The last area, being intermediate between most of Europe and most of Asia, could have received that part of its present flora which is not autochthonous from either continent; and it is well known that extensive migration occurred from both Asia and Europe into this region. Accordingly, in seeking an indication of the probable region of origin of *Crepis* on the basis of the present concentration of species, the intermediate region between Europe and Asia will not be considered as significant. Since in group I the number of species in Europe and Asia are equal, no inference can be drawn, on the basis of numbers alone, whether one or the other continent was the more probable region of origin of *Crepis*. When, however, we consider the relative primitiveness of the species, we find the European group to be on the whole the more primitive. This group includes *C. geracioides*, *C. viscidula*, *C. paludosa*, *C. pygmaea*, *C. lapsanoides*, *C. mollis*, *C. terglouensis*, *C. rhaetica*, *C. Jacquini* (all with $n=6$), and *C. aurea* ($n=5$); whereas the Asiatic group includes *C. kashmirica* and *C. lyrata* ($n=6$), *C. sibirica* ($n=5$) and *C. hokkaidoensis*, *C. chrysantha*, *C. gymnopus*, and *C. praemorsa* (all with $n=4$), as well as the tetraploid *C. polytricha* ($x=4$); also included are *C. tibetica*, *C. Gmelini*, and *C. elongata*, which are all more primitive than either *C. multicaulis* of Asia or *C. incarnata* of Europe. The chromosome numbers of *C. tibetica*, *C. elongata*, and *C. Gmelini* are not known, but they are probably either 5 or 6. Thus, the chromosome numbers show that the European group has more of the primitive species, a fact in agreement with the morphological evidence. On chromosome numbers and relative primitiveness of the species, the evidence from group I seems to favor Europe slightly as the probable region of origin.

TABLE 5

DISTRIBUTION OF THE RHIZOMATOUS SPECIES OF *CREPIS* (GROUP I)(Italicized names, being merely indicators of limits of distribution, are not counted in the species totals.)
(The number following each species is the haploid chromosome number.)

Section	Europe, north and middle: Mountains and plains	European Alps, including Pyrenees	Balkan Peninsula and Crete: Mountains	Asia Minor, Caucasus, W. Persia, Mountains	Eurasia, northern Plains and mountains	Asia, Central and east: Mountains
1	<i>sibirica</i> ←		<i>geracioides</i> 6 <i>viscidula</i> 6		<i>sibirica</i> 5 paludosa 6	→
2						
3		<i>pygmaea</i> 6				kashmirica 6
4		<i>terglouensis</i> 6 <i>rhaetica</i> <i>Jacquini</i> 6 ←		<i>albiflora</i> 4 <i>dioritica</i> →		<i>hokkaidoensis</i> 4 <i>chrysantha</i> 4 <i>polytricha</i> 8
5	<i>mollis</i> 6	<i>lapsanoides</i> 6	<i>smyrnaea</i> 6 <i>montana</i> 6 <i>Mungierii</i> 6	<i>willemetioides</i> 6 <i>hierosolymitana</i> 6		<i>lyrata</i> 6
13		←	←		<i>praemorsa</i> 4 →	<i>gymnopus</i> 4 →
21						<i>tibetica</i> <i>Gmelini</i> <i>elongata</i>
	<i>multicaulis</i>				<i>multicaulis</i> 4	
No. of species	1	5	7	4	4	9

Totals: Europe, including western Eurasia (*C. paludosa*)

Asia Minor, Caucasus, western Persia . . .

Asia, including eastern Eurasia (*C. sibirica*).

14 — 47 per cent.

4 — 13 per cent.

12 — 40 per cent.

30 — 100 per cent.

This evidence, however, must be considered along with the evidence from groups II and III; and, what is more important, the distribution of *Crepis* must be viewed in relation to that of the nearest related genera before attempting to formulate the most acceptable hypothesis. Furthermore, after this hypothesis has been set up, it must be reconsidered in the light of what is known concerning the origin and migration of floras in Europe and Asia.

Group II (table 6) includes the 109 more primitive taprooted species, of which 28 (26 per cent) occur in Europe and northwestern Africa, whereas 35 (32 per cent) occur in Asia and North America. It will be noted again that the species of Asia Minor, Caucasus, and western Persia are not taken into account in comparing concentrations in Europe and Asia, since they could have come from either region. For the same reason the species of the Mediterranean littoral and of tropical and south Africa are also ignored at this time; although, as is shown elsewhere (see p. 109), the probability is actually better that these African species migrated from Asia rather than from Europe. Of the 28 European and northwest African species (table 6), 7 have $n = 5$ and 14 have $n = 4$ chromosomes, 1 polyploid has $x = 5$, and of the 6 remaining, which have not been studied cytologically, none is likely to have more than 5 pairs and most of them probably have 4. Of the 35 Asiatic and North American species, 3 have $n = 7$, 3 have $n = 4$, 1 tetraploid has $x \times 4$, 10 polyploids have $x = 11$, and 18 have not been studied cytologically. Of these 18, 4 in section 12 very probably have $n = 7$, and all the others probably have either 5 or 4 pairs. On the basis of chromosome numbers in group II, the Asiatic species are definitely more primitive than the European species. But morphologically they are almost evenly balanced, the primitive species of Europe, *C. pontana* and *C. blattarioides* (sec. 6) and *C. albida* (sec. 7), being offset by *C. subscaposa*, *C. darvasica*, *C. songorica*, *C. turcomanica*, *C. khorassanica*, *C. orcadensis*, *C. ircutensis*, and *C. Bungei* of Asia, together with the 8 fairly primitive species of sections 16, 17, and 18, which have none comparable to them in Europe. From group II, therefore, the evidence on chromosome numbers and relative primitiveness of the species favors Asia as the region of origin to about the same degree that the evidence from group I favors Europe.

Comparable evidence from group III (table 7) can hardly be considered as significant as that from groups I and II because most of the species are advanced and, regardless of their present location, may have been derived from either Asia or Europe. Of the 18 species in Europe and northwest Africa, 17 are advanced species, 14 of these being in sections 23–27. Only *C. patula* can be considered as fairly primitive. Of the 6 species in Asia and adjacent northeast Africa, 4 are in section 20 and 2 in section 27.

On the basis of numbers of species alone, the distribution for the entire genus may be summarized as follows:

	Number of species	Per cent of total
Europe and northwestern Africa.....	59	30
Asia and North America.....	54	28
Asia Minor, Caucasus, western Persia.....	34	17
Africa, tropical and south.....	28	14
Mediterranean littoral and Canary and Madeira Islands.....	21	11
	196	100

The numbers in Europe and in Asia and North America combined can hardly be considered as significantly different. Added to this is the fact that Europe as a whole has been thoroughly botanized, whereas the mountains of Asia as a whole

TABLE 6

DISTRIBUTION OF THE MORE PRIMITIVE TAPROOTED SPECIES OF CREPIS (GROUP II)
 (Italicized names, being merely indicators of limits of distribution, are not counted in the species totals. The number following each species is the haploid chromosome number.)

Section	European Alps (secs. 6 and 8): Lower altitudes (sec. 10)	Spain-Italy, Morocco: Montane	Balkan Peninsula, including Crete: Montane	Asia Minor, Syria, Palestine: Montane
6	<i>pontana</i> 5 <i>conyzaefolia</i> 4 <i>blattarioides</i> 4		<i>conyzaefolia</i>	<i>conyzaefolia</i>
7		<i>albida</i> 5		
8	<i>alpestris</i> 4			<i>alpestris</i>
9		<i>tingitana</i> 5 <i>leontodontoides</i> 5		
10	<i>biennis</i> <i>pannonica</i>	<i>latialis</i> 4 <i>chondrilloides</i> 4 — <i>Triasii</i> 4 <i>oporinoides</i> 4	<i>bertiscea</i> -----→ <i>Baldaccii</i> 5 <i>auriculæfolia</i> <i>biennis</i> 20 10 others 5, 4	<i>bupleurifolia</i> <i>macropus</i>
11		<i>Hookeriana</i> 4 <i>Faureliana</i>	<i>Schachtii</i> 5 ←-----	<i>pinnatifida</i> <i>bithynica</i> 5 <i>Robertioides</i> 4
12				
14				
15				
16				<i>frigida</i>
17				
18				
No. of species	4	9	15	6

Totals: Europe and northwestern Africa (4 + 9 + 15). 28 — 26 per cent.
 Asia Minor, Caucasus, western Persia 17 — 15 per cent.
 Asia and North America (24 + 11) 35 — 32 per cent.
 Africa, tropical and south 28 — 26 per cent.
 Mediterranean littoral 1 — 1 per cent.
 109 — 100 per cent.

TABLE 6

(Continued from facing page.)

(For totals of numbers of species arranged in accordance with areas of distribution, see bottom of table on facing page.)

Caucasus region and W. Persia: Montane	Asia, from E. Persia and Turkestan eastward: Montane	Africa, tropical and south: Montane (mostly)	Mediterranean littoral	North America: Montane (mostly)
<i>conyzaefolia</i>	<i>conyzaefolia</i>			
<i>elymaitica</i>		<i>achyrophoroides</i>		
	<i>subscaposa</i>	24 species, six have 4		
			<i>suberostris</i> 5	
<i>Strausii</i> <i>sonchifolia</i> <i>ciliata</i> 20 <i>dens-leonis</i> <i>pannonica</i> 4	<i>darvasica</i> <i>songorica</i> <i>khorrassanica</i> <i>turcomanica</i> <i>pannonica</i>			
<i>armena</i> <i>heterotricha</i> <i>demavendi</i>	<i>oreades</i> 4 <i>crocea</i> 8	<i>tenerrima</i> <i>xyloirrhiza</i> <i>abyssinica</i>		
	<i>nana</i> 7 <i>flexuosa</i> 7 4 others			<i>nana</i> <i>elegans</i> 7
	<i>ircutensis</i> <i>Bungei</i> 4 <i>tectorum</i> 4			
				<i>monticola</i> 11 9 others 11
<i>sahendi</i> <i>purpurea</i>	<i>connexa</i> <i>elbrusensis</i>			
	<i>napifera</i>			
	Phoenix 4 others			
11	24	28	1	11

TABLE 7

DISTRIBUTION OF THE MORE ADVANCED TAPROOTED SPECIES OF CREPIS (GROUP III)
(Italicized names, being merely indicators of limits of distribution, are not counted in the species totals. The number following each species is the haploid chromosome number.)

Section	Europe: Lower altitudes	Spain-Italy, Algeria- Tripolitania: Montane (mostly)	Balkan Peninsula, including Crete: Lower altitudes	Asia Minor, Syria-Palestine: Lower altitudes
19			Stojanovi 4	Reuteriana 4 4 other spp. 4
20	<i>foetida</i>	← — — — —	rubra 5 — — — — — ← — — — — tybakiensis	<i>alpina</i> syriaca 5 → — — — — foetida 5
22	<i>sancta</i>		← — — — —	sancta 5 — — — — —
23		patula 4 ← — — — —	Dioscoridis 4 ← — — — — Zacintha 3 — — — —	multiflora 4 → — — — —
24	<i>capillaris</i> 3	<i>nicaeensis</i> ← — — — —	<i>nicaeensis</i> 4 neglecta 4 fuliginosa 3 2 other spp. 4	insignis
25	← — — — —	Claryi — — — — —	vesicaria 4	
26	<i>setosa</i>	amplexifolia 4	setosa 4 — — — — —	— — — — — aspera 4
27		bellidifolia 4 bursifolia 4		
No. of species	1	5	12	11

Totals: Europe and northwestern Africa	18	—	32 per cent.
Asia Minor and Caucasus region	13	—	23 per cent.
Asia and adjacent northeastern Africa	6	—	10 per cent.
Mediterranean littoral and oceanic islands	20	—	35 per cent.
	57	—	100 per cent.

TABLE 7

(Continued from facing page.)

(For totals of numbers of species arranged in accordance with areas of distribution, see bottom of table on facing page.)

Caucasus region: Lower altitudes	Asia, from Persia and Turkestan eastward: Lower altitudes	Africa, northeastern and S. Arabia: Montane	Mediterranean littoral	Madeira and Canary Islands
alpina 5 -----	-----→ Thomsonii 5	Schimperi eritreensis 5		
foetida	Kotschyana 4			
-----	-----→			
	parviflora		parviflora 4 apula 4 Suffreniana 4	
Marschallii 4			spathulata Salzmannii Clausonis 4 4 other spp. 4	canariensis 4 divaricata 4 Noronhaea 4 vesicaria
→			juvenalis 4 aculeata 4 2 other spp. 4	
		Rueppellii Forskalii	nigricans 4 filiformis senecioides 4	
2	2	4	17	3

have been comparatively little explored. It is safe to predict that numerous species of *Crepis* remain to be discovered in Asia as well as in Africa. In Asia, especially, it is not improbable that some of these undiscovered species are among the more primitive in the genus. But on the basis of existing evidence on numbers of species now occurring in Europe and Asia, it is impossible to draw any conclusion concerning which continent was probably the region of origin of the genus. However, the evidence on the distribution of closely related genera and on the distribution of species in the primitive sections of *Crepis* leads to a definite hypothesis.

THE DISTRIBUTION OF RELATED GENERA

In the subtribe Crepidinae, as defined by Stebbins (cf. p. 62), the larger or more critical genera, other than *Crepis*, and their present distributions are as follows:

1) *Dubyaea*, from which all the genera in the subtribe are assumed to have originated, and its close derivative, *Soroseris*, are restricted to the Sino-Himalayan region. That this was not their actual place of origin, or that of the Crepidinae, but rather that they probably moved in here from the Altai-Tien Shan region will be developed in the following chapter.

2) *Youngia* and *Ixeris*, the closest relatives of *Crepis*, are distributed in southeastern Asia, for the most part between the seacoast and the Pamir and Altai mountains, with *Youngia* extending more to the west and *Ixeris* more to the east and south (cf. Babcock and Stebbins, 1938). *Chondrilla* occurs in China and Siberia, but has become distributed as far west as Europe. *Taraxacum* has some of its most primitive species in southern Europe, some in Asia Minor, and many others in Central Asia. Handel-Mazzetti (1907) reached the final conclusion that this world-wide genus had its "cradle" in the "heart of Asia" and that this generalization agrees with others repeatedly obtained in analagous investigations. Such a definite conclusion by such an eminent authority, concerning a closely related genus with a comparable distribution, must be recognized as having an important bearing on the present problem.

3) *Prenanthes* has its present center of distribution in eastern Asia and extends into North America, Europe, and tropical Africa. In this connection it is of special interest, as was pointed out by Stebbins (1937b), that *P. subpeltata*, the only species of *Prenanthes* known from the African continent, "has its closest relatives in the temperate rain forests of the Sino-Himalayan region at corresponding altitudes." *Lactuca*, which is considered by Stebbins to be essentially monophyletic and yet "broad-based," i.e., derived from a group of rather diverse but interrelated species, has three main centers of distribution. One of these is southeastern Asia, another is Asia Minor and southeastern Europe, and the third is southwestern tropical Africa (Belgian Congo and Angola). The distribution of neither of these genera is adverse to the idea of an Asiatic origin; in fact, a Central Asiatic center is strongly indicated for both of them.

4) *Launaea* and *Sonchus*. The connection between these genera and *Dubyaea*, according to Stebbins, is obscure, but yet they certainly belong to this subtribe. The most primitive species are in northwestern Africa (Atlas Mountains), Spain, and the Madeira and Canary Islands. These genera are related to *Tolpis*, which is strictly European and north African. Hence, there is no clear evidence that either of these genera originated in Asia.

5) *Hieracium* is the most widespread of all the genera of the Crepidinae, but its most primitive species as well as the greatest range of variability and the strongest development of the genus are in central and northern Europe. *Tolpis* and some

other small genera close to *Hieracium* are primarily western Mediterranean genera, and, like *Launaea* and *Sonchus*, their most primitive species occur in Madeira and the Canary Islands.

From the foregoing review it appears that the general picture of geographic distribution in the Crepidinae suggests an Asiatic origin for *Dubyaea*, *Soroseris*, *Youngia*, *Ixeris*, *Taraxacum*, *Chondrilla*, *Prenanthes*, and *Lactuca*. Only in the *Hieracium-Tolpis* and the *Launaea-Sonchus* lines is the present distribution predominantly European. In *Launaea*, *Sonchus*, and *Tolpis*, the distribution of their most primitive species in the western Mediterranean region is strictly comparable to the occurrence in Spain and Italy of some of the most primitive species of *Taraxacum* and *Crepis*. It is only necessary to assume that the connection between those small western Mediterranean genera and *Dubyaea* is obscure because their more *Dubyaea*-like ancestors which lived farther to the east are now extinct. Considering its world-wide distribution, it would appear at first glance that a similar assumption might be made for *Hieracium*. But I am informed by Stebbins (oral communication) that all of the Asiatic species of subg. *Euhieracium* are apomictic. Furthermore, the American subgenera, *Stenotheca* and *Mandonia*, are specialized, derived groups. This evidence, together with the occurrence of the most primitive species in Europe, seems to favor a western Eurasian rather than a Central Asiatic origin for this genus. Nevertheless, *Hieracium*, like *Launaea*, *Sonchus*, and *Tolpis*, must be assumed to have originated from *Dubyaea* or *Dubyaea*-like ancestors.

In this connection, mention should be made of an alternative hypothesis concerning the possible region of origin and early migration of the ancestral stocks that produced the Asiatic and European lines of the Crepidinae. It is possible that the *Dubyaea*-like ancestors of these two groups of genera developed as a branch of the pre-Tertiary arctic flora in the region of the northern Ural Mountains. Then, in early Eocene time, before the Obic Sea separated Europe from Asia, certain *Dubyaea*-like plants which later gave rise to the *Hieracium-Tolpis* and *Launaea-Sonchus* lines migrated into northern Europe, where they continued to develop throughout the Tertiary period until they were driven southward or were exterminated by increasing cold; whereas the ancestors of *Dubyaea*, *Soroseris*, and the *Prenanthes-Lactuca*, *Youngia-Ixeris*, and *Crepis* lines migrated into north Central Asia and became established in the Altai-Tien Shan region. This assumed scheme is consistent with the facts concerning the present preponderance in Europe and the Mediterranean region of *Hieracium*, *Tolpis*, *Launaea*, and *Sonchus*, and with a Central Asiatic origin for the other larger genera of this subtribe. But this hypothesis assumes the differentiation of the *Dubyaea*-like ancestors of the Crepidinae into distinct *Hieracium*-like and *Crepis*-like forms by early Eocene, something which is difficult to imagine in the light of the history of the Angiosperms as a whole. The very earliest seed plants appeared only in the preceding period (Seward, 1941, p. 383). Furthermore, this scheme does not harmonize with the location and history of the Ural and the Altai in relation to Angara, which is, it seems, the most probable region of origin of the Angiosperms (see p. 93). The Altai has been a part of Angara Land since the Carboniferous period (see p. 95), whereas the Ural was completely cut off from this region by the Obic Sea from mid-Eocene to mid-Oligocene (see figs. 5 and 6). It seems more probable, therefore, that the whole subtribe Crepidinae had its origin in Angara and particularly in the Altai.

THE DISTRIBUTION AND CENTER OF ORIGIN OF
CREPIS SPECIES

The rhizomatous species.—The distribution of the species in the more primitive sections will now be examined with reference to the possible origin of *Crepis* in Central Asia, with the understanding that the western Altai and Tien Shan mountains are included in the area. Among the rhizomatous species, sections 1, 3, and 5 will first be examined, then sections 2 and 4. In section 1, *C. geracioides* and *C. viscidula* occur in the Balkan Peninsula, the former being lower montane in association and the latter subalpine or alpine. *C. geracioides* is definitely a southern species; and, since *C. viscidula* occurs only in Bulgaria and *C. geracioides* is its closest relative, it is also southern in its affinity. *C. sibirica* is a diminishing relic in the Carpathian region, is common in Russia and northern Asia from the Urals to Transbaikalia, and occurs in the mountains of western Mongolia and eastern Russian Turkestan. It is listed by Pax (1898, p. 226) as one of six flowering plants comprising a typical "Siberian" element in the flora of the Carpathian Mountains. *C. paludosa* extends throughout most of middle and northern Europe and into western Siberia. This species presents a special problem because of its intermediate character between *Crepis* and *Hieracium*. If it actually originated through hybridization between primitive members of those genera, as seems probable, the event could have occurred during a common migration into northern Europe through the Turgai region south of the Ural Mountains. The geological and vegetational history on which this statement is based is reviewed in chapter 6. At any rate, *C. sibirica* and *C. paludosa* probably migrated from Central Asia into Europe by some such northern route, whereas *C. geracioides* and *C. viscidula* must have taken a southerly route. That a route to the south and west was followed by *C. pygmaea* of southern Spain and the south-western Alps, and by seven of the eight species of section 5, is strongly indicated by the distribution of these seven species: one in Central Asia, one in northern Persia, one in Palestine, one in eastern Asia Minor and Greece, another in Greece, one in Crete, and one in the Pyrenees. *C. mollis*, the other member of section 5, is widely distributed in middle Europe, and it occurs mostly at low elevations. Its closest affinities are all southern. It is worthy of note that in this section, in which sufficient traces have been preserved, there is good conformity with Matthew's general principle. Only to the extent that *C. montana* of Greece and *C. Mungierii* of Crete are more reduced in size than *C. willemetiioides* of Persia, is there incomplete conformity with this principle. Furthermore, *C. lapsanoides* of the Pyrenees is certainly the most primitive species of this section.

The primitive *C. kashmirica* (section 2), like *Dubyaea oligocephala* and *D. hispida*, probably moved into the western Himalaya region from farther north in the late Tertiary or early Quaternary period. *C. kashmirica* is an alpine species occurring at altitudes from 3,500 to 4,300 meters; hence it could not have occupied its present area until postglacial time. From its present conditions of life, it appears that it could not have survived if it had ever started to migrate southwestward from Central Asia along the route which was probably followed by the primitive *Crepis* species of southern Europe.

In section 4 the relationship to an assumed center in Central Asia is beyond doubt. In nine species—one in northern Japan, two in northern Asia (one from Altai to Transbaikalia, the other from Altai to Kamchatka and on the arctic Eurasian tundras), two in Asia Minor, another extending from Asia Minor through the Balkan countries to Italy and the Alps, and the three most primitive species endemic in the Alps—we find a distribution that could hardly indicate more clearly a center

of distribution in Central Asia. This section also conforms with Matthew's principle which is summarized on page 75.

The evidence from sections 13 and 21 also strongly indicates an Asiatic center of distribution. In the first group, *C. gymnopus*, which is the most primitive of the three species, is endemic in Japan; *C. praemorsa* extends from Manchuria through Siberia to the Altai and from the Urals across Russia and middle Europe as far as Scandinavia and northern Italy; *C. incarnata*, which was evidently derived from *C. praemorsa*, is restricted to a small area in northeast Italy, southeast Switzerland, southern Austria, and the western Balkan Peninsula. In the last section, *C. tibetica* and *C. elongata* occur in eastern Tibet, western Szechuan, and northern Yunnan, and *C. Gmelini* is in eastern Siberia. All three are definitely more primitive than the polymorphic *C. multicaulis*, which extends from the western Himalayas through the mountains of Turkestan to the Altai Mountains and occurs in a small district in northeastern Norway. This district, Varanger in Finmarken, is part of that narrow strip of northernmost Scandinavia which, according to both Hulten (1937) and the Great Soviet world atlas, Pt. I (1937, cf. Hobbs, W. H., Science 104 [2692]: 106, 1946), was not covered by Pleistocene ice. Evidently, this species, like *C. sibirica* and *C. paludosa*, migrated from Asia into northern Europe.

The more primitive taprooted species.—Turning next to the more primitive taprooted species we find in section 6 four species that differ rather strikingly from one another in distribution. *C. pontana*, the most primitive, occurs in the western European Alps and southeastward in the mountains of the western Balkan Peninsula at elevations from 1,200 to 2,500 meters. *C. blattarioides* occurs from 700 to 2,200 meters in elevation in the Pyrenees, throughout the Alps, and in the western Balkan Peninsula. These two species occur mostly on limey soils. The occurrence of these alpine and subalpine relics in southern Europe may at first appear to throw doubt on the probability of their origin in Asia, especially since they have been recognized by some European botanists as part of the autochthonous flora of the Alps (cf. Diels, 1910). It happens, however, that one other species in this section provides the stations by which the origin of this section can be traced back to Central Asia. *C. conyzaeifolia*, which is next in degree of primitiveness to *C. pontana*, occurs from the Pyrenees through the Alps to the Balkan Peninsula and Carpathian Mountains, also in northern Asia Minor, Transcaucasia, northern Persia, and the Altai Mountains. Although often mentioned as a subalpine or alpine species, it is known to occur between 600 and 3,000 meters, and its usual altitudinal range is from 1,000 to 2,000 meters. Furthermore, this species flourishes on soils deficient in lime, including schists; and it has been reported in sterile meadows on dry sod and in open swampy woods. Evidently, it is a much more adaptable species than the other three, and this probably accounts for its ability to persist in places along the route of migration from the assumed center of origin to its farthest outpost in the Pyrenees.

Section 7 includes three species with interesting distributional relations. *C. albidula*, the most primitive one, is a polymorphic, lower montane species distributed mostly in Spain, with outlying stations in southern France, northwestern Italy, the Balearic Islands, and northern Morocco. The next most primitive species, *C. achyrophoroides*, is endemic in northern Abyssinia, and the most advanced species, *C. elymaitica*, is known from only two collections in the high mountains of western Persia. Even in this small group, on the assumption that the center of origin was in Central Asia, we again find excellent conformity with Matthew's principle.

Section 8 is the next in size to the largest section in the genus and, except for two species, *C. alpestris* and *C. subscaposa*, it is distributed entirely in tropical and south Africa. The first-mentioned is distributed in western Asia Minor, the western

Balkan states, the Apennines, the eastern Alps, and the western Carpathian Mountains. On the basis of the characters used for sectional delimitation, *C. alpestris* belongs in this group. At the same time it exhibits considerable morphological resemblance to *C. conyzaefolia*, the widespread member of section 6. Like *C. conyzaefolia*, too, it has a wide altitudinal range, 500 to 2,650 meters; but it usually occurs on limey soil which may have a bearing on its failure to occur farther eastward. At any rate, *C. alpestris* is actually a connecting species between the two sections and serves as a good indicator of the probable development of section 8 from the same center of origin as section 6. *C. subscaposa* of southwestern China, northwestern Burma, and western Indo-China is closely similar throughout to the species of the larger, more advanced subsection of section 8. So far as is known, it has no close relatives in Asia, its resemblance to the anomalous *C. napifera* being limited to the root, the caudical leaves, and the erect, nearly leafless stem, whereas the type of inflorescence, size of heads and number of florets, involucre characters, and surface of the receptacle, as well as the flowers and fruits, all resemble those of the African species. Hence, *C. subscaposa* and *C. napifera* must represent widely divergent lines which probably arose from the same ancestral stock. *C. subscaposa*, therefore, adds considerable weight to the evidence from *C. alpestris*, showing that the twenty-six species in section 8 all stem originally from a Central Asiatic source. *C. subscaposa* is one of the more advanced species in this section and *C. alpestris* one of the most primitive, but *C. kilimandscharica* and *C. keniensis* of the two highest mountains of northeastern tropical Africa are both more primitive than *C. alpestris*. Hence, in this section also we find general conformity with Matthew's principle.

The three species in section 9 all occupy areas in the western Mediterranean region, but the most primitive species, *C. tingitana* of Spain and Morocco, is farthest to the west. *C. leontodontoides* is intermediate, but, as was indicated by the results of hybridization experiments, is still fairly primitive. It is distributed in western Italy, Sardinia, Corsica, and southern France. *C. suberostris*, an advanced, annual species, occurs on the western Algerian littoral and adjacent upland. These geographical relations fit in well enough with the general picture of distribution in the genus with reference to an Asiatic origin.

In both sections 10 and 11 the range of distribution is just as consistent with an Asiatic origin as it is in the widely distributed sections already discussed (see table 6). The fact that some of the most primitive species in both sections occur in Turkestan and Persia, whereas others are found in the Caucasus and Balkan regions, is understandable on the basis that they, being actually less primitive groups than those discussed above, have had less time and opportunity to become dispersed sufficiently to conform closely with Matthew's principle. This principle, however, was found to apply well to the distribution of sections 3, 4, 5, 7, 8, and 9. Furthermore, section 6 is in general agreement with it; and we have seen that the restriction of section 2, *C. kashmirica*, to very high altitudes in the western Himalayas is sufficient in itself to explain the failure of this species to get farther from the assumed center of origin. On the other hand, the persistence of *C. sibirica* (sec. 1) in the exact region of the assumed center of origin is certainly an exception to Matthew's principle. But this is a widespread species; whereas *C. geracioides*, which is even more primitive in some respects, is a local endemic situated far from the assumed center.

The Asiatic sections, 12, 16, 17, and 18, together with the North American extension of section 12 and the wholly American section 15, are all in perfect agreement with the hypothesis that the genus originated and was dispersed from Central Asia.

The most advanced species.—Finally, the most advanced sections of *Crepis* are all distributed in the Mediterranean region, some of them extending as far east as northwestern India and Turkestan, and some occurring as far west as Madeira. This concentration of the most advanced sections in the general region of the Mediterranean Sea is wholly consistent with the hypothesis that the ancestors of these species came from Central Asia. The highest development of the genus in this region is a natural result of the topographic and climatic changes that have taken place there since Tertiary times.

CONCLUSION

This review of the geographic distribution of *Crepis* species and of the genera closest to *Crepis* leads very definitely to the conclusion that the center of origin and early development of *Crepis* was in Central Asia, probably in the Tien Shan–Altai region. Further consideration is given to this hypothesis from the standpoint of geology, paleobotany, and vegetational history in the following chapter.

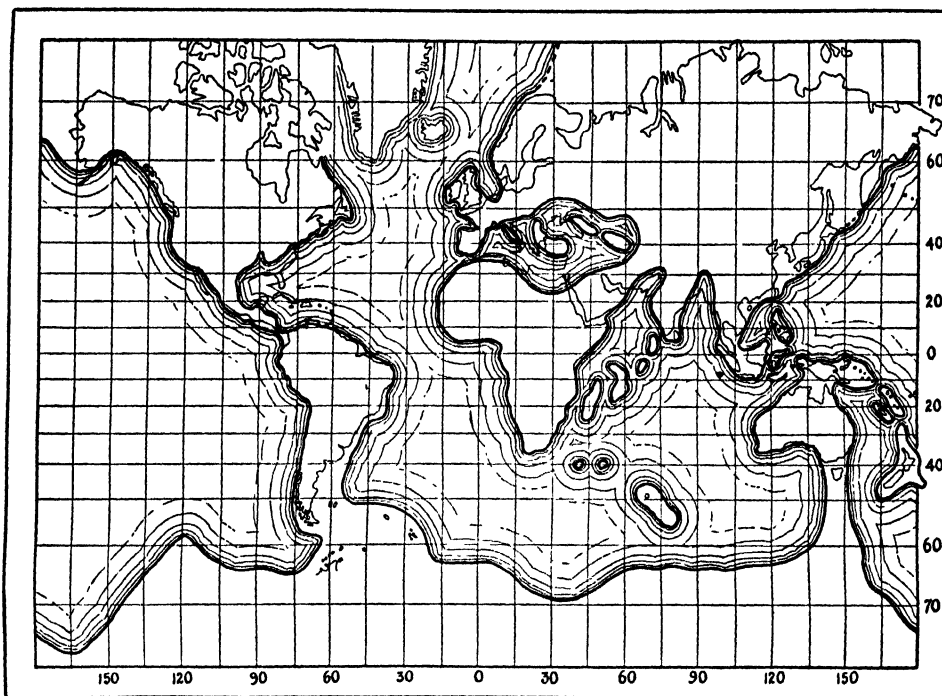
CHAPTER 6

ASIATIC-EUROPEAN PLANT MIGRATION AND ITS BEARING ON THE PRESENT DISTRIBUTION OF CREPIS

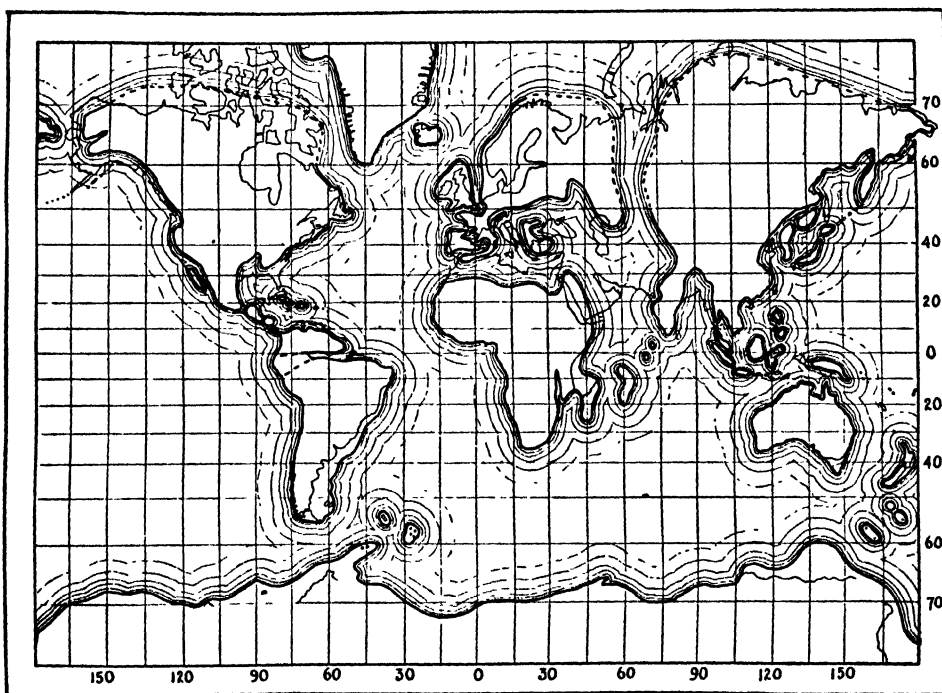
BEFORE PROCEEDING to describe the probable course of development of *Crepis*, it is necessary to examine the general background of floristic history in Eurasia since the Mesozoic era. In attempting to envision the general aspects of the development and migration of Eurasian flowering plants, the author has consulted numerous treatises on the distribution of extinct and living species. The Tertiary fossil record in Europe is rich and the literature correspondingly extensive. In addition to the well-known book of Seward (*Plant Life through the Ages*, 1941), there are fortunately a number of excellent general reviews of this literature as well as some fairly recent reports of investigations by competent authorities in this field. A very helpful general view of the geological history of Asia was found in *The Structure of Asia*, edited by J. W. Gregory (1929); and the works of Fickeler (1925) and of Berkey and Morris (1927) on the geology of Altai and Mongolia have provided valuable supplementary information. Matthew's standard works on Tertiary continental outlines and climate and evolution have, of course, been invaluable aids. In addition to these books, numerous papers have been consulted. In basing assumptions on the evidence in some of these papers, it is realized that there is a certain element of risk in relying on the identification of fossil plant materials. For this reason, in questions of critical importance I have tried to use evidence from paleobotanists of widely recognized standing, although this has not always been possible. With the help of this literature I have attempted in this chapter to give, in as brief form as possible consistent with clarity, a general picture of earth history in Eurasia since the Mesozoic era, with special reference to the development and migration of the flowering plants, particularly of *Crepis*. Since completing Part I of this monograph, Wulff's excellent work, *An Introduction to Historical Plant Geography* (1943), has come to hand. It is reassuring to find that the principles and methods adopted by the present author are in close agreement with those advocated by Wulff, especially in connection with the location of centers of origin and the migrations of species. The theory of continental drift (Wegener, 1924) need not be considered in connection with the origin and migrations of *Crepis*, since this is essentially a northern group which must have migrated into Africa during the Tertiary period.

CONTINENTAL OUTLINES IN THE TERTIARY PERIOD

Geologists are in general agreement that important changes in the outlines of the continents occurred during the Tertiary period. These changes are clearly indicated on the six maps prepared by Matthew (1906) which are reproduced in figures 5-7. Carefully prepared from the best geographical, paleontological, and zoölogical data available at the time, it is probable that these maps are in the main fairly dependable; although, as Matthew states: "The European continent presents a very complicated problem and considerable parts of the outlines shown must be admitted to rest on pretty slender evidence." Thus, the relative *widths* of the seas separating Europe and Africa, as well as Europe and Asia during certain intervals, may be subject to some modifications; but the fact that such seas existed and their relative positions are much more pertinent to the present discussion than their

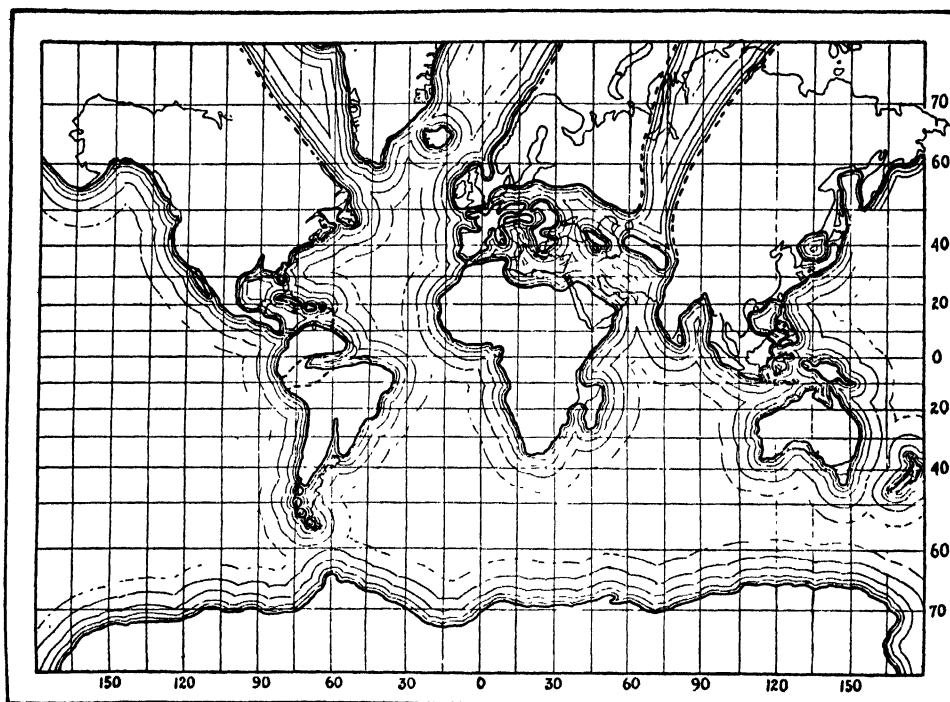


HYPOTHETICAL CONTINENTAL OUTLINES—POST-CRETACEOUS

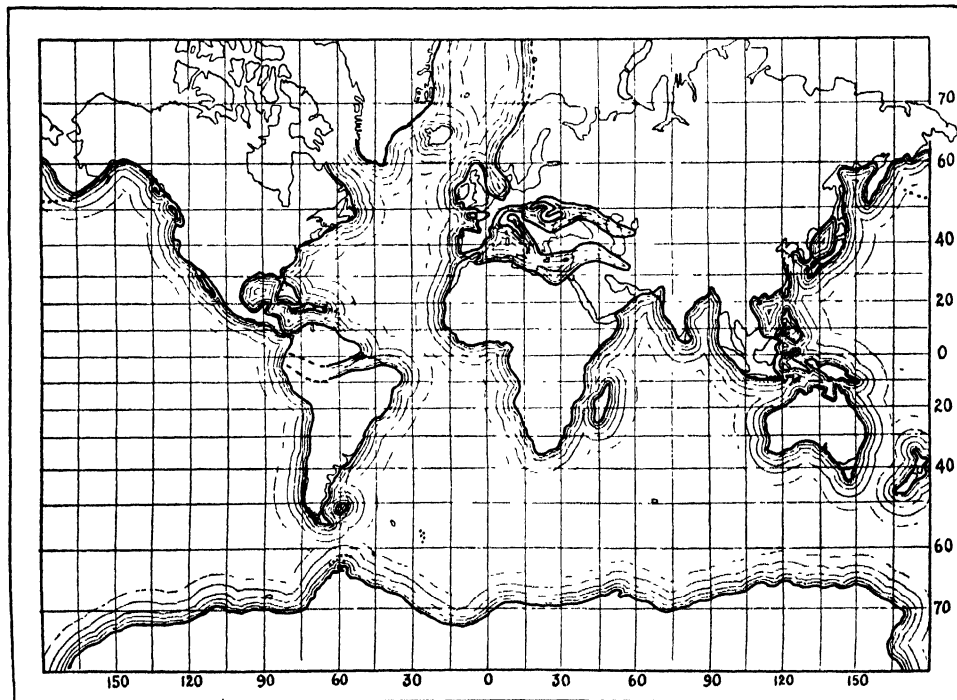


HYPOTHETICAL CONTINENTAL OUTLINES—MIDDLE EOCENE

Fig. 5. Maps 1 and 2 of Matthew's hypothetical continental outlines—post Cretaceous (above) and Middle Eocene (below).

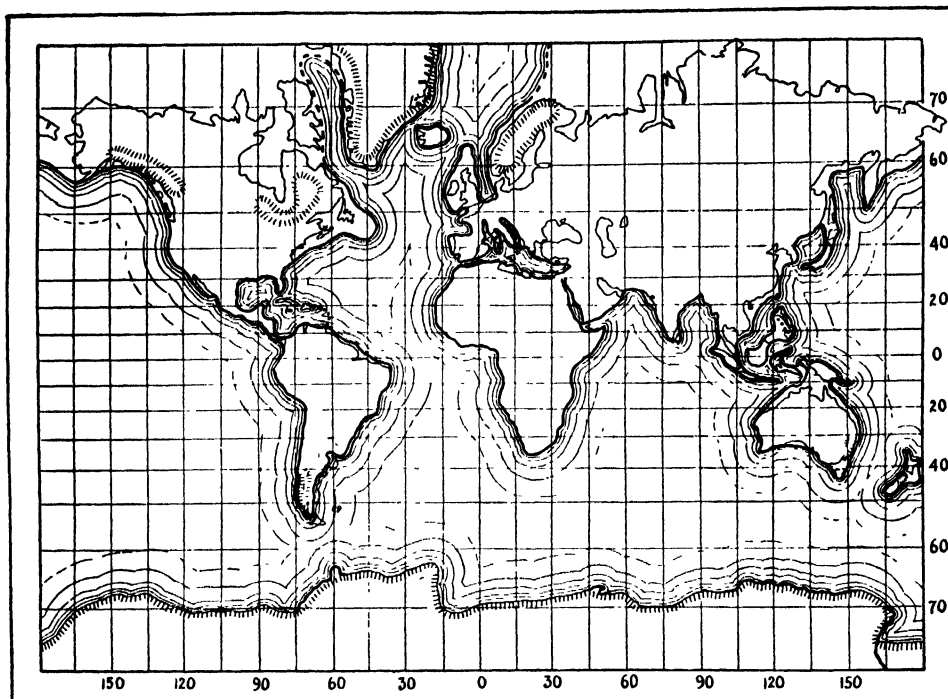


HYPOTHETICAL CONTINENTAL OUTLINES—MIDDLE OLIGOCENE

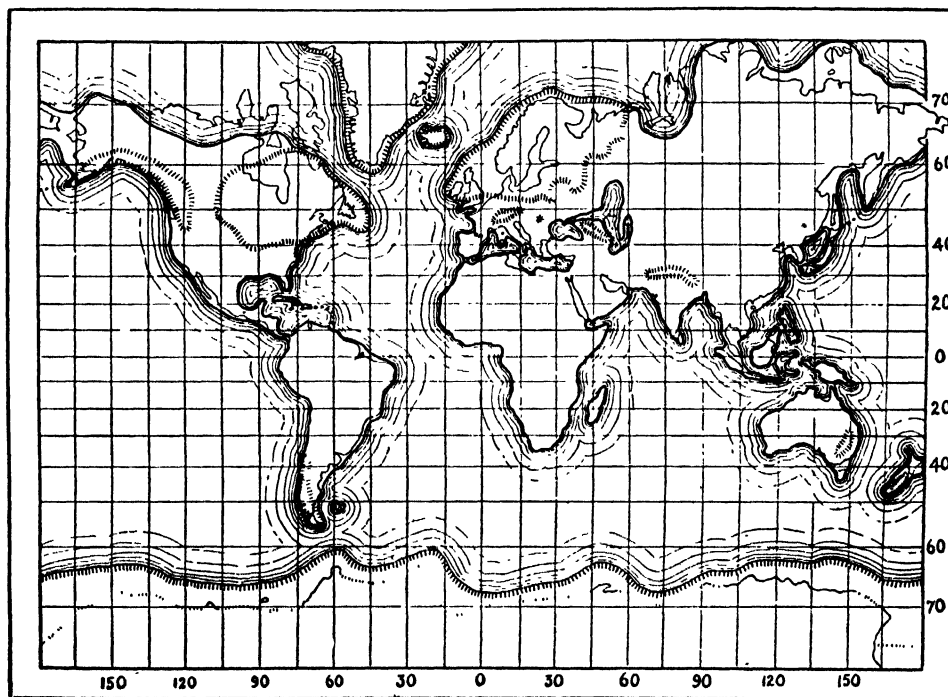


HYPOTHETICAL CONTINENTAL OUTLINES—MIOCENE

Fig. 6. Maps 3 and 4 of Matthew's hypothetical continental outlines—Middle Oligocene (above) and Miocene (below).



HYPOTHETICAL CONTINENTAL OUTLINES—PLIOCENE



HYPOTHETICAL CONTINENTAL OUTLINES—EARLY PLEISTOCENE

Fig. 7. Maps 5 and 6 of Matthew's hypothetical continental outlines—Pliocene (above) and early Pleistocene (below).

approximate sizes. The high lights of the six consecutive geological ages represented by the maps have been condensed from Matthew's description, with some added notes on floras based on Seward (1941). It is to be remembered, of course, that the whole process of earth history is continuous and the best that can be done in a brief series of descriptions is to note the points of most significance for the problem in hand.

Post-Cretaceous.—During and after Cretaceous there was a great extension of the sea over land areas, the continents were isolated, and oceanic climate probably extended mild, moist conditions widely over the lands. It was the age of reptiles. At its end there was a great upheaval in both the Northern and Southern Hemispheres, with great intermigrations. Old faunas and floras vanished and mammals and flowering plants appeared.

Middle Eocene.—The sea again insulated the six great land masses. *Europe and Asia were separated east of the Ural region by the "Obic Sea."* Each continent then developed a peculiar fauna. That the climate was warm, moist, and equable is indicated by the record of plant fossils which reveal the existence of dense forests over large areas. Herbaceous plants were relatively few.

Middle Oligocene.—The continents had partly emerged and Asia and North America were connected by a broad area in the north. But South America, Africa, and Australia remained separate. Europe and Asia were still separated by the Obic Sea; but this barrier to plant migration was removed, at least in part by the end of Oligocene.

Miocene.—The continents had emerged further, somewhat reducing Tethys, the great central sea of Europe and Asia. But this now consisted of two great arms that reached eastward beyond the present Caspian Sea. *And it is worth noting that the peninsula separating these two arms included part of Iran (Persia) and the Caspian region, the northern part of Asia Minor and part of the Balkan Peninsula, and northern Italy, thus making a complete land connection between Asia Minor and southern Europe. In the north Asia and Europe were continuous; and Asia was still connected with North America through "Beringia."* This connection persisted until Pleistocene. *Africa was connected with Asia across Arabia,* thus permitting extensive intermigration of plants and animals. The latter part of this age probably brought the increase of cold climate at the poles, with its gradually increasing effects upon the general trends of plant migration in the Northern Hemisphere. North and South America were not yet completely connected.

Pliocene.—Elevation of all the continents continued generally, but Africa was again nearly cut off by the Red Sea. South America was united with North America. Tethys was reduced almost to the present size of the Mediterranean Sea. Probably the great elevation of northern Eurasia and northeastern America and the increasing polar cold initiated the glacial epoch in Greenland, Labrador, and Norway, with consequent increasing plant migration from north to south.

Early Pleistocene.—The culmination of glaciation marks this period. Matthew's map does not show the area of maximum glaciation completely (cf. Hulten, 1937). During early Pleistocene the Black, Caspian, and Aral seas were united into the huge Hyrcanian Sea. Asia Minor and the Balkan Peninsula were continuous land. The Mediterranean was separated into two closed seas, i.e., there was one land connection across the Straits of Gibraltar and another connecting Tunisia, Sicily, and Italy. Africa was again connected with Asia by all of Arabia. These facts are all of significance in connection with the present distribution of *Crepis*.

RELATIVE AGES OF THE THREE CHIEF MOUNTAIN SYSTEMS OF ASIA AND THE MOST PROBABLE REGION OF ORIGIN OF CREPIS

In the following discussion no pretense is made to a critical analysis of the many problems connected with the relative ages of individual mountain ranges in Asia. Some of these problems are discussed by the various authors represented by contributions in the *Structure of Asia*, edited by J. W. Gregory. Among these and various other authors cited, there seems to be general agreement on the thesis that there were three distinct periods of mountain building in this continent; and, by a brief review of these different periods of orogenic activity and their chief results, it is hoped to throw a little more light on the problem of the general region of origin of *Crepis*, particularly whether it was more probably in the northern, central, or southern part of Asia.

The oldest mountains in Asia are the remnants remaining of the so-called "primitive nucleus" of Suess (1901) or the "archaic old vertex" of Fickeler (1925). The western, southern, and southeastern margin of this region is indicated by the line of dots and dashes in figure 8. This U-shaped range, situated in what is now the Lake Baikal region of Siberia, was upfolded as early as the Paleozoic era (cf. F. E. Suess, in Gregory, 1929, p. 36); and it may well have played an important role in the early history of the evolution of higher plants in Asia by providing new types of environment. Such an inference is in keeping with the views expressed by Seward (1941, p. 279), as follows: "The rich plant beds of Siberia, which include Carboniferous, Permian and Mesozoic strata, are still very imperfectly known. The more we know of the plants preserved in the older Permian rocks and in the beds classed as Permo-Triassic in China and Korea, the more promise there seems to be of discoveries which will enable us to reconstruct some of the missing links in the chain of plant life connecting the Paleozoic and Mesozoic floras. There are indications that the original home of many genera characteristic of the earlier Mesozoic vegetation may have been in the continent of Angara (= northeastern Asia), a region which has been preëminently immune from the disastrous consequences of geological revolutions." And, again (*op. cit.*, p. 290): "The late Paleozoic vegetation derived its characteristic features from floras composed in great part of extinct types, whereas among the plants of the late Triassic floras we at once recognize the precursors of more familiar and more modern forms. The preliminary steps in this transformation were taken in the latter part of the Paleozoic era." This view agrees with that of Gothan (1930), who points to eastern Asia as the region of origin of the flowering plants.

These general ideas of Seward and Gothan concerning the importance of Angara as a region for the development of new floras during the Mesozoic and Cenozoic eras have been supplemented by Kryshstofovich (1933) in his study of the Baikal formation of the Angara group. Through the kindness of M. K. Elias, who translated parts of this paper for me, the following brief generalization is a dependable statement of Kryshstofovich's views: (1) In Permian time certain elements of the Gondwana flora moved into more northern latitudes. In Asia they mingled with elements of the European flora which had become changed under the influence of desiccation; and together these gave rise to the Mesozoic flora of Angara. (2) In mid-Cretaceous time the composition of the flora of Angara continent radically changed. This new Cretaceous vegetation, the Angiosperms, probably came from the north. That they had a circumpolar distribution is shown by the existence of systematically and biologically similar forms in the floras of the Potomac region (eastern United States), of Souchan (Russian Far East), and of Portugal. (3) Be-

tween early and late Cretaceous there occurred a great oceanic flooding of Angara continent from the east and, when parts of the continent once more rose above sea level, they were populated anew by an entirely different flora in which the Mesozoic relics were, for the most part, exterminated. A temporary marine transgression

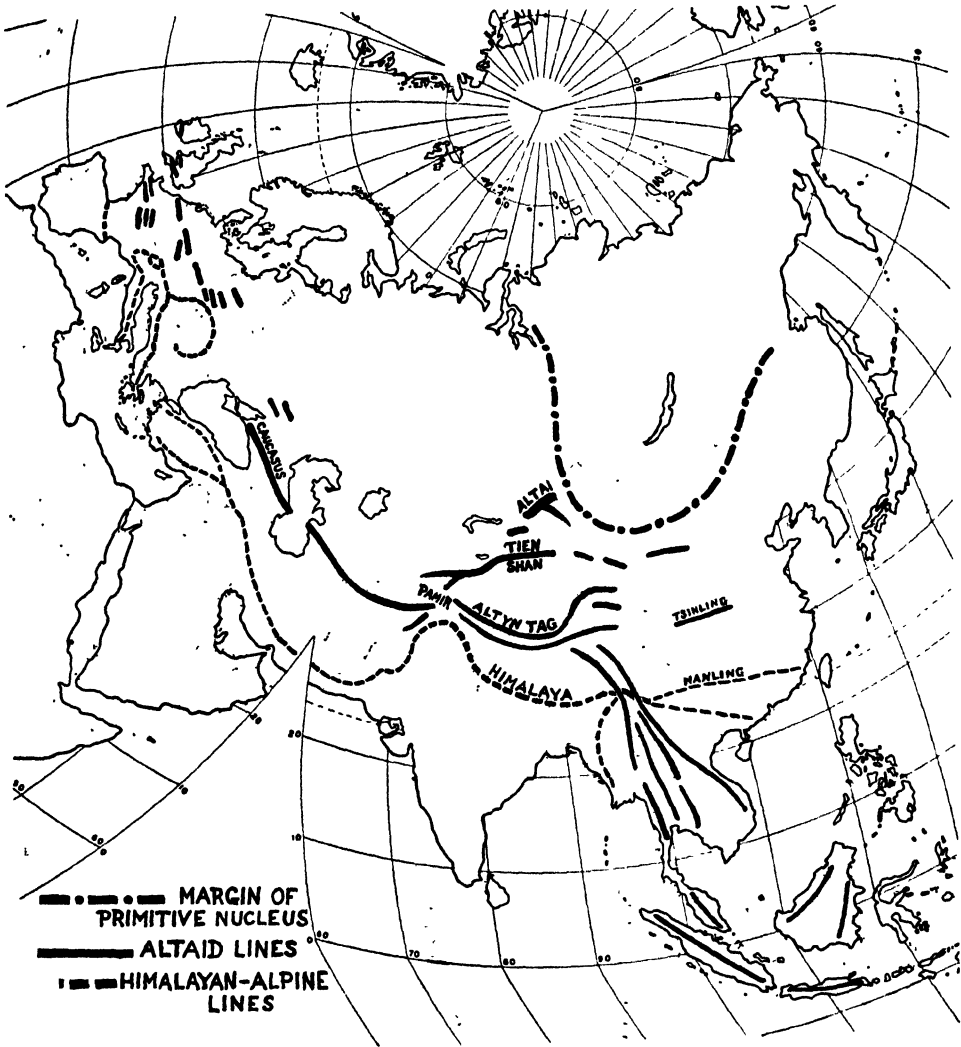


Fig. 8. Diagrammatic representation of the three principal systems of mountain chains in Asia, the Primitive Nucleus, the Altaids, and the Himalayan-Alpine system, and the extensions of the last two in Europe. (Copied from fig. 2 in Gregory's *The Structure of Asia* with slight modification.) Based on Goode Base Map No. 201 PC. By permission of the University of Chicago Press.

could not possibly cause the evolution of new forms of plant life; but it was sufficient to eliminate some species of plants, thus giving space for others, creating new edaphic conditions, and eliminating competitors in the struggle for existence.

Although the primitive mountain nucleus of northern Asia may have been an important factor in the *early* evolution of the floras of the present day, yet it can hardly have been so important in the middle and later periods of that long continuum. By the middle of the Paleozoic era these mountains, according to Barbour

(in Gregory, 1929, p. 195), were already greatly reduced. Since erosion probably continued throughout the Mesozoic era, by the dawn of the Tertiary period they must have been relatively unimportant topographically.

The next important mountain-building period in Asia produced the western Altai and Tien Shan mountains, several nearly parallel east-west ranges lying to the south and southeast of the Tien Shan-Fergana system, also a series of ranges extending eastward from Tien Shan, and several nearly parallel chains running southward from eastern Tibet and western Szechuan through the Malay Peninsula, as well as the Ural and Caucasus mountains, and the Variscan and American horsts of Europe. These Altaid systems are shown by solid black lines in figure 8. Recurring movements were involved in the formation of these mountains. These movements began toward the end of the Paleozoic era and recurred from time to time through the Mesozoic era (cf. Cotta, 1871, p. 299; Fickeler, 1925, pp. 173-181; Nekhorosheff, 1932, pp. 23-24; Karakin and Korniliev, 1935; Javjarov, 1935; Murchison et al., 1845, pp. 408, 464; Volfson, 1940). Each of these great systems has a complex history, marked by epeirogenic movements alternating with periods of rest. For example, Berkey and Morris (1927, p. 314) discuss the history of the Artsa Bogdo Mountains, an eastern extension of the Altai range. They conclude that this part of the Altai system was uplifted and peneplaned during or before Lower Cretaceous time. They also report evidence of faulting and tilting, recurring since that time at such long intervals that the relief features due to faulting were planed away. Nevertheless, unlike the almost completely eroded Variscan and American horsts extending across middle Europe from west to east, which correspond in age with the Altai and Tien Shan, these mountains of Central Asia still rise to great heights (up to 4,500 meters in the Altai and to nearly 7,000 meters in the Tien Shan) and contain many glaciers. According to Fickeler (1925, p. 174), the Russian Altai has remained a part of the Asiatic continent from the Carboniferous period to the present time (see also Murchison et al., 1845, p. 499). The combined effects of epeirogenic movements and erosion have left the highest points in the original fault-mass ranging from 2,000 to 2,300 meters high in the Russian Altai and from 2,000 to 3,700 meters in the Mongolian Altai. Furthermore, the same author (*op. cit.*, pp. 176-177) states that the Altai was twice as high in the Paleozoic era as in the Tertiary period. Even in the Mesozoic the elevation of the Russian Altai must have been 5,000 meters. Tertiary tectonic processes brought new climatic relations, resulting in the contrast between the central dry region (Mongolian Altai) and the peripheral humid region (Russian Altai). Superimposed on this great contrast were still greater climatic variations. For example, in the South Altai a subtropical flora is found in Lower Pliocene deposits. Fickeler concludes (*op. cit.*, p. 182) that in the Altai living things find a starting point. Plant geography shows it to be the native home of a flora that radiated far into Europe, a flora of which gigantic representatives still charm the eye of explorers in the Altai, whereas to Europeans, only their dwarfed forms are known.

Thus it has been possible for the Altai to serve as a favorable region for the continuous evolution of plant phyla at least up to Pleistocene times when heavy local glaciation may have destroyed some, but not all, of the alpine autochthonous species which had not already migrated southward. In this connection I am indebted to C. W. Sharsmith for pointing out the basic fact "that glacial phases are the most favorable climatically for the flourishing of true alpine (or arctic) species in the region of origin, where areas free of ice occur." For this reason, further exploration of the Altai-Tien Shan Mountains will probably reveal other primitive

species of *Crepis* as well as *Dubyaea* and *Soroseris* (see p. 82). The point to be emphasized here is that in northern Central Asia there was available all through the Tertiary period a region of highly diversified topography and a temperate climate where the ancestors of the Cichorieae could have developed and produced such primitive Cichoriaceous genera as *Dubyaea*, which in turn produced the most primitive species of *Crepis* and numerous other genera.

The third great mountain system lies to the south and consists of the Nanling, Himalayan, and associated ranges, which correspond roughly in age with the mountains of Iran, Asia Minor and the Balkan Peninsula, the Alps, and the Pyrenees. These mountains are indicated by lines of short dashes in figure 8. This series of high ranges was formed during a long period of vast orogenic activity, including volcanic eruptions which began mostly in Oligocene. By mid-Miocene some of these great ranges, for example the Alps, were fairly well developed; but the general process of mountain formation along this great axis continued throughout the Pliocene and into Pleistocene or even Recent times. According to Schwarz (1938), the Himalayas were elevated in late Pliocene and Pleistocene and the Pamirs and Hindu Kush and the mountains of Asia Minor even later. Regarding Asia Minor, Syria, and especially Iran, however, it has been shown by Böckh, Lees, and Richardson (in Gregory, 1929, Chap. III, pp. 153-168) that orogenic movements began in this region as early as the Paleozoic era and that the main movements occurred in Pliocene times. From this it follows that most if not all of these mountains of the south, from the Nanling-Himalayan system to the Alps and Pyrenees, were in stages of development suitable for colonization and migration by plants being driven southward by increasing cold during Pliocene.

But the relic species of *Dubyaea* and *Soroseris*, which are endemic in southeastern Asia and the western Himalaya region, probably spread into those regions from Central Asia early in the Miocene epoch, if not earlier (cf. Stebbins, 1940, pp. 73 and 75). According to Stebbins (*op. cit.*, pp. 51-52), these primitive relatives of *Crepis*, like many other relic alpine species of southwestern China and eastern Tibet, appear to be remnants of a flora which was formerly more widespread but was largely destroyed by Pleistocene glaciation. Most of the relic *Dubyaea* species now occur, with many other relics, on or near the Altai mountain ranges of eastern Tibet and western Szechuan. *D. hispida* is distributed westward through the Himalaya, but this probably resulted from post-Pleistocene dispersal. Stebbins (*op. cit.*, pp. 52-53) also points out that *D. oligocephala*, another primitive species, like *Soroseris Gillii* subsp. *occidentalis* and *S. Deasyi*, occurs only in the western Himalaya and adjacent regions, and that this disrupted distribution between closely related species of southwestern China and western Himalaya is characteristic of a number of genera (cf. Diels, 1913). Most of the *Soroseris* species have a wider distribution than the *Dubyaea* species, either in southwestern China, or in western Tibet, the western Himalaya, and Sinkiang. Thus, the distribution of the genus *Soroseris* as a whole (cf. Stebbins, *op. cit.*, p. 54, fig. 14) may logically be interpreted as indicating a Central Asiatic origin and center of distribution. In this connection it should be noted that *S. Deasyi* apparently exists now in the middle Tien Shan Mountains. One herbarium specimen (*Deasy 95*, BM, UCf) has only "Aksu" and "5000 m" on its label. But the town of Aksu is at an elevation of only 1,000-1,500 meters, whereas the Aksu River just to the north rises in the middle Tien Shan. Since the other four elevations at which this species is known to occur are all over 4,000 meters, it is much more likely that this specimen was collected in the high mountains than on the plateau. To the present author, one collection of a single *Soroseris* species in the Tien Shan Mountains is very significant, since it

shows that one of these relic species now exists in the region assumed, on other grounds, to be the center of origin of *Crepis*.

The nine species of *Crepis* now known from the Sino-Himalayan region represent but four different sections (8, 17, 18, and 21), only one of which, section 18 with five species, is well developed in this area. The other four species certainly appear to have migrated into this region from elsewhere (cf. Stebbins, 1940, p. 73); and it is highly probable that all nine of these species, or their ancestral forms, followed the same general route from the Altai-Tien Shan region as that taken by the ancestors of *Dubyaea* and *Soroseris*. Referring again to figure 8, it is clear that the Altai mountain ranges radiate in a general southeasterly direction to the Malay Peninsula, thus providing a route from Central Asia to the present locations of most *Dubyaea* species; also that the congested series of ranges between the Tien Shan and the Himalaya would provide ample opportunity for the dispersal of wind-borne seeds. All in all, the present distributions of *Dubyaea*, the genus representing the ancestors of *Crepis*, and of the closely related genus, *Soroseris*, fit in perfectly with the hypothesis that the center of origin and dispersal of *Crepis* and its ancestors was in Central Asia.

THE DIVERSE TERTIARY FLORAS OF ASIA AND EUROPE

Kryshtofovich (1929), in discussing the evolution of Tertiary floras, shows that the Tertiary floras of eastern Europe and Asia belong to different floristic provinces. The principal floristic boundary line, he states, runs across northern Europe from southeast to northwest, separating the temperate flora of Arcto-Tertiary composition on the north from the subtropical and tropical flora of southern Russia, Ukraine, and the rest of Europe. The Crepidinae and the whole tribe Cichorieae are temperate and arctic, not tropical, lowland species. One would not think of tropical, early Tertiary Europe, therefore, as the region of origin of this group of plants. Kryshtofovich separates the Tertiary-Temperate region into the western Greenland Province, which includes the north Ural Mountains and probably adjacent Europe and Asia, and two great eastern provinces. One of these, the North Siberian Province, included northern Alaska. According to Kryshtofovich, the flora of this province shows resemblance to the older Greenland flora as well as to the earliest Cretaceous flora of the Laramie type found in Amur and Bureja; and of the latter it is clearly a descendant. In this connection Kryshtofovich remarks that, in parts of Asia, plants seem to have developed without interruption since they started from their primeval Cretaceous prototypes. The other great Asiatic temperate region recognized by Kryshtofovich as having existed during Tertiary is the Turgai Province, the vast "middle zone" of northern Turkestan, Siberia, Manchuria, Korea, Sakhalin, and Hokkaido, also most of Alaska and probably Arctic America and Greenland. It should be noted that although Chaney (oral communication) is not convinced that two distinct northern Asiatic Tertiary provinces should be recognized by different names, yet this "major classification of the Tertiary vegetation of Eurasia by Kryshtofovich" has been accepted by Chaney and Hu (1940, p. 109).

During the first half of the Tertiary age, at least until Lower Miocene, this region was covered with a uniform, deciduous forest in which amentiferous species predominated. Interestingly enough, many of the primitive *Crepis* species are found today associated with amentiferous trees; such species as, for example, *C. geracioides*, *C. lapsanoides*, *C. kashmirica*, *C. lyrata*, and *C. mollis* are known to be associated with such trees. Although this proves nothing, still it does show that some species of *Crepis* could have evolved in just such an association. Furthermore,

the Turgai Province area includes the western part of the Altai Mountains, which certainly existed throughout the Tertiary and which was a region of great diversity in topography and climate. Regarding the general trend of the climate in Central Asia during the Tertiary period, Chaney (1935, p. 96) has made the suggestion, based on a comparison of Miocene floras from western Siberia, the Altai, and southern Russia, that there was a gradual reduction in rainfall and probably in temperature in this region throughout the whole Cenozoic era.

TRENDS OF TERTIARY PLANT MIGRATION IN ASIA OF SIGNIFICANCE FOR *CREPIS*

The combined evidence from fossil plants and the geographic distribution of living species shows that during the Tertiary period there were four major routes of plant migration in Asia. One of these routes connected the region of northern Central Asia and North America by way of the Beringian land bridge. Over this route there was intermigration between the two continents; but the northeasterly trend from Central Asia into North America was undoubtedly the direction followed by *Crepis*. Another movement was a general southeasterly one from northern and Central Asia toward Korea, Japan, China, and the Malay Peninsula. Still another trend was in a southwesterly direction from Central Asia into southern Europe and northern Africa. Later in its beginning than the other three was the westerly migration from Central Asia across the steppes south of the Ural Mountains into northeastern Europe. These four distinct migration trends are indicated on the map in figure 9. The pointed directional lines are intended merely to show the general direction of what must undoubtedly be thought of as radial mass movements from the general region of Angara and Central Asia. No pretense is made here to a complete review of all the available evidence bearing on this vast subject. But it is hoped that in the following discussion sufficient evidence will be presented to warrant the foregoing generalization and to provide a dependable background for the hypothetical history of *Crepis* which has been based mainly on phylogenetic and distributional evidence.

The northeasterly trend from Angara and Central Asia.—Recognition of an important trend of plant migration from northern Asia can be made without definite commitment with respect to the actual region of origin of the species involved. As was indicated by Seward (1941) and Kryshstofovich (1933), the ancestors of the Tertiary arboreal and herbaceous species of the Northern Hemisphere may have originated in Angara. But in the latter part of the Cretaceous period both Eurasia and North America were elevated and became continuous with the Arctic Continent (fig. 5, map 1). This could have made possible the holarctic distribution of many conifers, of which *Sequoia* is an outstanding example (Chaney, 1940), and such primitive angiospermous trees as *Magnolia*, *Platanus*, and *Quercus* (Seward, 1941, pp. 389–391), and *Cercidiphyllum* (Chaney, 1938, pp. 377–378). By middle Eocene, however, both Europa and Angara were once more completely insulated (fig. 5, map 2); and it was not until mid-Oligocene that Arctica was again lifted above the sea and that Asia was again united with North America. Hence, it seems much more probable that it was in mid-Tertiary time that such warm temperate genera as *Cedrus* and *Datisca* must have migrated from Asia into North America. That this was the direction of migration, rather than vice versa, is certainly indicated by the present distributions of both genera which resemble that of *Crepis*.

Schwarz (1938) explains the present distribution of the genus *Cedrus* as due to the interrelations of diverse old floras which met in the Mediterranean region. Nevertheless, the distribution of the four species appears to the author to be con-

sistent with the assumption that the genus originated in northern Asia; *C. deodara* in northwest Himalaya, Afghanistan, and northern Baluchistan; *C. libanitica* in southern Asia Minor and Liban; *C. brevifolia* in Cyprus; and *C. atlantica* in Algeria and Morocco. Furthermore, such fossil evidence as exists is not necessarily inconsistent with this assumption. According to Pilger (1926), *Cedrus* fossils have

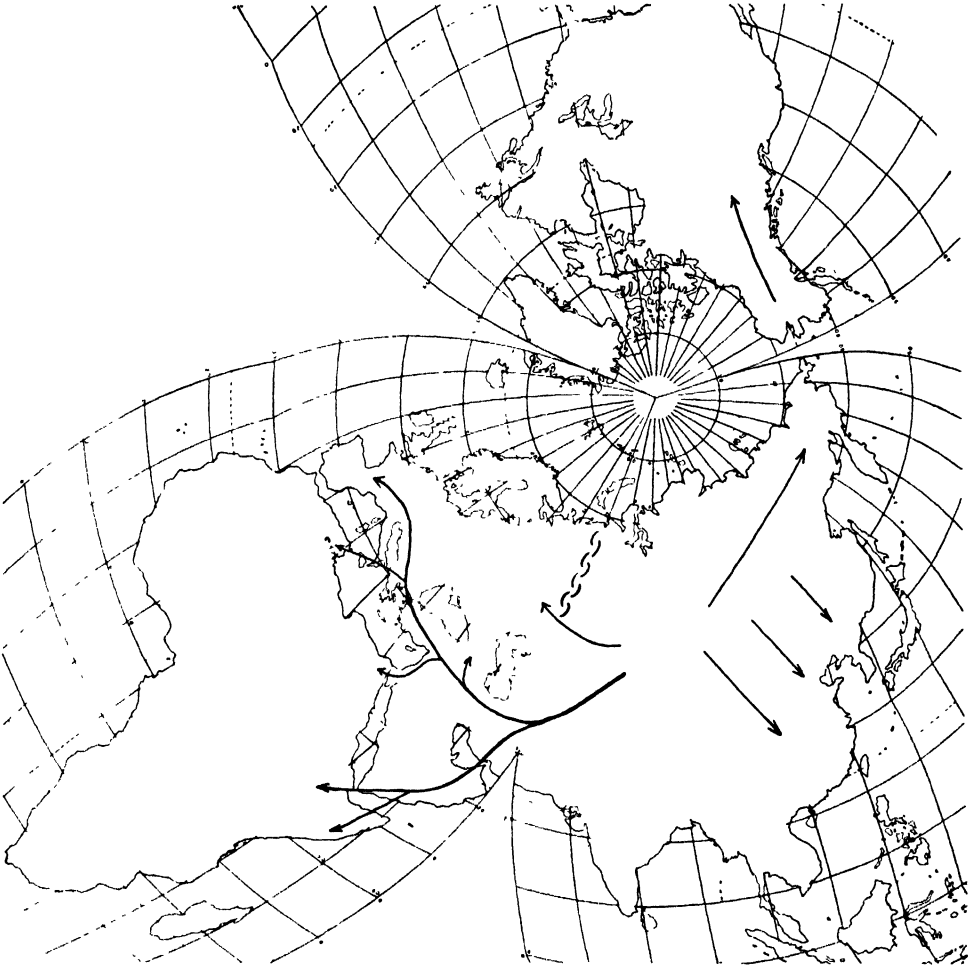


Fig. 9. Map showing the four trends of Tertiary plant migration of most significance for *Crepis*: (1) northeasterly from northern Asia into North America; (2) southeasterly from northern Asia; (3) southwesterly from Central Asia into southern Europe and northern Africa; (4) westerly from Central Asia across the southern end of the Ural Mountains into northeastern Europe. Fossil evidence shows that all of these trends, except the fourth, began before the assumed migration period of *Crepis*; and *Crepis*, like many other younger groups, followed similar routes. Based on Goode Base Map No. 201 PC. By permission of the University of Chicago Press.

been reported from Cretaceous deposits in western Europe and from Tertiary deposits in France and Germany, as well as in eastern Siberia. The last-mentioned locality, from the original report (Heer, 1878), is actually in south-central Siberia, about 100 kilometers west of Krasnojarsk. There, in a Miocene deposit, were found cone scales, seeds, and leaves of a species which Heer states is undoubtedly closely related to *C. deodara*. Recently, well-preserved specimens of *Cedrus* wood have

been discovered in Tertiary auriferous gravels in California (Barghoorn and Bailey, 1938). The wood in these specimens, being neither mineralized, nor lignitized, nor carbonized, can be distinguished from that of existing species of *Cedrus* by the absence of ray tracheids; and a similar difference exists between certain fossil pines and existing species.

Although it must be admitted that the oldest known fossils of *Cedrus* are from western Europe, yet similar or older records may eventually be discovered in Asia. One thing is certain, that during Tertiary the genus was distributed in Europe, Asia, and North America. Furthermore, in an extensive review by Schwarz (1938) it was concluded that such arboreal genera as *Cedrus*, *Pinus*, and *Quercus* represent the primary Mediterranean flora which came from Asia (see p. 106). A similar inference is drawn by Markgraf (1934, p. 71) concerning the Asiatic origin of certain species of *Pinus* and *Picea*. Thus, it appears that northern Asia or adjacent Arctica may be considered as the probable region of origin for *Cedrus*. This is in line with the general conclusion of Seward (1941, pp. 387, 400) that the origin of the conifers of the Northern Hemisphere was in the arctic region. From the known fossil record of *Cedrus*, it would appear to have originated in the Asiatic rather than the American Arctic.

In her critical study of the problem of the Pontide (a hypothetical land connection across the Black Sea joining Asia Minor and Crimea), Czecczott (1937) points out that the heavy rainfall which occurs in northern Anatolia and the absence of barriers against plant migration across northern Asia Minor are of great importance in explaining present-day plant distribution in that region and to the west. The problem of the Pontide is of only minor significance for *Crepis*; but some of the studies of the Colchic-south Euxine plants made by this author are very convincing in respect to the plants having an Asiatic origin and having migrated both eastward and westward. Among these are *Datisca cannabina* and *Fagus sylvatica*.

Although the other genera of the Datisceae inhabit tropical India and the Sunda Islands, *Datisca cannabina* is a temperate species, occurring up to 3,000 meters altitude. This species is found not only in Colchis (the district at the eastern end of the Black Sea and south of the Caucasus) but also at isolated stations in southern Asia Minor, Syria, and Crete, as well as in northwestern Persia, Afghanistan, eastern Turkestan, Kashmir, and India. Czecczott points out that the Colchic flora is inseparable from the sea; and, therefore, it must be assumed that these inland stations were situated near a sea at some past epoch. It is known (cf. Mushketov, in Gregory, 1929, pp. 177, 185) that in eastern Turkestan (Ferghana) the sea lasted until Upper Oligocene times. Ancient Tethys persisted from Cretaceous to Oligocene and extended across western, northern, and central Persia. During Lower Miocene, when lagoon conditions set in and formed thick beds containing salt and gypsum, extreme desiccation took place (cf. Gregory, *op. cit.*, Chap. III). In Upper Miocene, only a narrow gulf penetrated into central Persia from the Persian sea (*ibid.*, Chap. VIII). From this evidence Czecczott infers that the gap between the eastern and western parts of the distribution of *Datisca cannabina* resulted from the dryness of the climate in the Miocene epoch and that this species is not younger than Upper Oligocene. This she states is confirmed by the fossil remains found between Turgai and the Aral Sea which are considered as Oligocene deposits by Abich and Kryshstofovich. The survival of *D. cannabina* from that remote period is correlated with the plasticity shown by its great vertical distribution, from sea level to 2,000 meters in Colchis and from 300 to 3,000 meters in Kashmir. Finally, the only other species of this genus, *D. glomerata*, is found in California and Mexico, occurring up to 1,500 meters altitude in the California

mountains. Like *D. cannabina*, it is a temperate, not a tropical species. These facts concerning *D. cannabina* and its closest relatives certainly indicate a Central Asiatic origin for the group.

Fagus sylvatica L., the common beech, is one of the Colchic-south Euxine trees mentioned by Czechtz as abundant and aggressive in that region. The general distribution of this species includes—in addition to northern Anatolia, Pontus, and Lazistan—the Persian province of Astrabad, southeast of the Caspian Sea; also it is widely distributed in middle Europe and in southern Europe—in northern Greece and Albania, Istria, the southern base of the Alps, the Apennines, Sicily and Corsica, southern France in the Cevennes Mountains, the eastern Pyrenees, and northern Spain. In the southern Balkan Peninsula and in the Pyrenees this tree has associated with it such primitive *Crepis* species as *C. geracioides* and *C. lapsanoides*.

Fagus is one of the many genera which are much older than *Crepis*, but which appear to have originated in Asia or the Arctic region to the north of the present continent of Asia, and which seem to have followed a developmental and migrational history somewhat similar to that of *Crepis*. Even though *Fagus* were holarctic in distribution at one time, this does not preclude its having originated in Angara or adjacent Arctica. The other existing members of the genus *Fagus* are *F. Sieboldii* and *F. japonica* of Japan and *F. grandifolia* of eastern North America.

According to Prantl (in Engler u. Prantl, 1894, 3[1]: 53, 54) various fossil forms of *Fagus* are known in Cretaceous and Tertiary deposits; and some of them extend the earlier distribution of the genus to Alaska, Washington, Oregon, and California, as well as to Spitzbergen, Iceland, and Greenland. Without a critical study of adequate fossil specimens of both this and related genera, it would, of course, be impossible to determine whether *Fagus* originated in Angara or Arctica. Kryshstofovich (1935), however, describes *F. Antipovii* as "definitely archaic," and this is one of the characteristic species of the Tertiary flora that covered the vast region extending from northern Turkestan and southern Siberia eastward. This fossil species has also been found in Alaska. It is true, therefore, that primitive forms of *Fagus* were distributed continuously across Siberia and North America to Greenland and Iceland late in the Cretaceous period. It has been shown by Kryshstofovich (*op cit.*) that *Fagus Antipovii*, like many other species of the temperate Tertiary Siberian flora which developed during late Cretaceous in Asia and possibly in the Arctic, migrated westward and southwestward, reaching Europe during the Miocene epoch.

In their studies on the Pliocene flora of Bulgaria, Stefanoff and Jordanoff (1935) found the Fagaceae second only to the conifers in relative abundance. *Fagus orientalis* Lipsky, the fossil beech which they found, is believed to be the parent form of *F. sylvatica* L., the common beech of today. It, therefore, may be considered, at least in a general sense, as a connecting link between the latter and certain more primitive species, like *F. Antipovii* of Siberia and Alaska.

Thus, the distribution of *Fagus* in Tertiary times indicates a history of development and migration in general similar to that of *Datisca cannabina*, the salient features of which are probable Asiatic origin and migration eastward into North America and westward into Europe. That these features also characterize the history of *Crepis* will be made clear in chapter 8.

The southeasterly trend from northern Asia.—That the southeasterly trend of Tertiary floral units across both Eurasia and North America is an expression of continentality essentially like that now controlling the distribution of living forests in the Northern Hemisphere was first pointed out by Chaney (1940). Chaney and

Hu, in their study of a Miocene flora from Shantung Province, China, find "evidence of a southward migration of the temperate forest in eastern Asia corresponding to that between Alaska and Oregon between Eocene and Oligocene." They also cite other evidence supporting a "southward movement of vegetation during the epochs following the Eocene" in eastern Asia. They attribute this "migration of the temperate flora from high northern to middle latitudes by Oligocene time" to geographic changes involving "the draining of the Obie Sea which connected the Arctic Ocean with Tethys during the Eocene, and perhaps the withdrawal of other meridional seas which had facilitated the transfer of warm waters into high latitudes." With the further great reduction in size of Tethys from Miocene to Pliocene, it is safe to assume that this north-south trend of migration of vegetation in Asia extended farther westward. The significance of this migration trend for the history of *Crepis* has already been indicated (p. 97) in the discussion of the present distribution of the supposed ancestors of *Crepis* (or their living representatives) in the mountains of southeastern Asia.

The southwesterly trend from Central Asia.—The importance of this trend in Asiatic-European plant migration was fully appreciated by Engler (1879). In his detailed treatment of the development of the high montane flora before, during, and after the glacial period, he derives among others the following generalizations. (1) The genera represented by alpine and high alpine species in the Himalaya are for the most part the same as those represented by alpine species in the Pyrenees and Alps. (There are five primitive *Crepis* species which occur only in the Alps and the Balkan Peninsula; whereas there is none which occurs only in the Altai. But several of the most primitive species, namely, *C. sibirica*, *C. chrysantha*, *C. lyrata*, and *C. conyzaeifolia* occur in the Altai; and their distribution indicates that they were dispersed from the Altai.) (2) When the few representatives occurring in the Alps also occur in the Altai, in addition to relatives of the same group, their origin in Asia is decided. (Of the four *Crepis* species mentioned above as occurring in the Altai Mountains, *C. conyzaeifolia* also occurs in the Pyrenees and the Alps as well as in northern Asia Minor, Transcaucasia, and northern Persia. *Crepis* is also represented in the Alps and Pyrenees by other primitive species and in the Himalayas by four alpine species, one of which, *C. kashmirica*, is one of the most primitive species in the genus.) (3) Worthy of greatest consideration is the fact that, of the plants of the Altai and other parts of Siberia, several, such as *Aconitum anthora*, *Saussurea discolor*, and *Pedicularis comosa*, certainly occur in the Alps and Caucasus, but not in Scandinavia. This shows that part of the plants that migrated from Siberia to the Caucasus and Alps went apparently in a southwest direction to the Mediterranean mountains and not through Scandinavia. This land, at least at the height of the glacial epoch, was not suitable; otherwise, since there were high arctic plants that migrated to the Caucasus, Carpathians, and Alps, some at least could have existed in Scandinavia, as some do today as far north as the eightieth meridian. (This explanation of Engler's is inconsistent with his statement [below] that he knows of no evidence for as great glaciation as in the Alps; but it in no way detracts from the cogency of his evidence in support of the southwesterly migration from Central Asia.) The other Siberian glacial plants that occur in the western Alps, eastern Alps, and Carpathians appear mostly in the eastern Alps and Carpathians as a result of the first colonization by Siberian plants. (This "first colonization by Siberian plants" was apparently hypothetical on the part of Engler. Strong evidence that it actually occurred has been reported by Kryshtofovich [1935].) (4) From the distribution of the plants of the Altai and alpine Himalaya we can generalize concerning the migrations that went on in Central Asia. In the

Himalaya as well as the Altai the same genera occur; and the number of species in both of these two regions generally is smaller than the number of species that occur in both the Mediterranean mountains (including the Alps) and the Altai. The mountains south of Altai connecting the Altai with the Himalaya have developed their endemic montane flora from the steppe elements of the lower regions, as have the mountains of the Mediterranean peninsula. On the Pamir plateau and on Tien Shan, glaciation probably had a great effect, as it also probably did in the northwest Himalaya. But Engler states that he knows of no evidence, and this has been verified by others, for as great glaciation as in the Alps (cf. map of maximum glaciation of Hulten, *op. cit.*; also Cotta, 1871; Karakin and Korniliev, 1935; Javjarov, 1935). Fewer areas were therefore opened for colonization than in the Alps (this obviously applies to *Crepis*). The actual migrations of the flora from Afghanistan, Persia, and Turan occurred after Miocene time, when moisture gradually decreased and the climate became drier. Western Asia became the reservoir of relic mesophytic vegetation and, gradually, more and more steppelike. Steppe animals occurred in the higher parts throughout the whole region and could easily have carried seeds from Altai to Himalaya and from these mountains to western Tibet, Afghanistan, Turan, Songoria, and Ala-Tau; but here, according to Engler, because it would not be so easy for the seed to produce progeny, the terrain generally developed nearly related forms (referring presumably to the origin of vicariant species from the original migrants); whereas north from the Caucasus, the Carpathians, and the Alps, the plants growing in longer summers, through their retreat to the south or by complete extinction, gave place to the species coming from the east.

Some of Engler's ideas on the migration of high montane plants, further elaborated in a much later publication (Engler, 1916), are so applicable to *Crepis* that they will be mentioned here.

1) The assumption that vicarious species remnants represent former polymorphic types with a wider continuous area finds an obstacle when it concerns species with claims to special climatic and ecologic relations and which occur only in high mountains that are separated by wide plains or seas. There are two possibilities: (a) An older long since extinct stem species has lived at the foot of the mountain area in Tertiary; and at different points in its area, with conditions sometimes varying and resembling those in high mountains, mutations have resulted in parallel forms or vicarious varieties which developed into species. (b) Seeds of species A, growing under high montane conditions, were spread by birds or winds from mountain to mountain; and in the new locations there occurred mutations, $A^* = B$, $A' = C$, which remain as relic species.

2) From polymorphic types, groups of species are gradually developed which are, ecologically: (a) groups in which there are forms at present in hilly country with a short winter near higher regions with a long winter; (b) groups containing only species in regions with a very long winter and short summer. From old Tertiary elements of the lower regions, by successive mutations, new species were formed at the upper limits which have passed into higher regions with harsher climates.

3) For the hypotheses of plant migration in general, the transportability and length of vitality of the seeds are to be considered, as well as the climatic conditions under which a group of species flourishes today. (With reference to *Crepis*, these points are discussed in chapter 8.)

4) For the estimation of the possible migrations in the glacial period and especially for the preservation of species in areas subject to glaciation, it is not unimportant to know how high species go up in the higher regions and how low they

come down in the lower regions. (All available data on the altitudinal range of *Crepis* species will be found in Part II; see also the altitudinal distribution of the endemic species of *Crepis* in the following chapter.)

Engler's conviction concerning the derivation of important elements in the high montane flora of southern Europe through southwesterly migration from Central Asia have been corroborated by Braun-Blanquet (1923). Braun-Blanquet's reply to the question whether our representatives of the original flora of the Alps migrated into the Alps unchanged is that *phylogenetic and phytogeographic research compels the question to be answered unconditionally in the affirmative*. The Tertiary basic stock of the alpenflora, according to this author, was derived chiefly from Mediterranean and middle Asiatic stems and migrated into the Alps partly from surrounding lower country and partly from neighboring older mountains. During the Pliocene age new endemic forms developed. In addition to the Mediterranean and middle Asiatic stems, three less important components are mentioned by Braun-Blanquet as contributing to the high montane flora of southern Europe. The northern flora, which came in from the northeast during the Ice Age, decreases in importance in the Alps from northeast to southwest. The Sarmatic flora (Sarmatia is the region north of the Black Sea), considered broadly, has contributed species which characterize the dry valleys of the coniferous zone in the central Alps. The west European or Atlantic flora is very scantily represented in the Alps in contrast to the mountains of middle France and the Pyrenees.

Similar conclusions had already been reached by Braun-Blanquet (1921-1930) as a result of his exhaustive study of the present and fossil floras of the mountains of central France, where he recognized three principal elements: the Eurosiberian-Boreoamerican, the Mediterranean, and the Aralo-Caspian. The first of these is subdivided into three subelements: the middle European, which is autochthonous, the Atlantic, and the Boreoarctic. Although his classification of the woody-stemmed species under these elements is presumably correct, it may be that future research on the herbaceous species will necessitate some changes. Of the five species of *Crepis* reported, for example, none is referred to the Eurosiberian element. It is very probable, however, that *Crepis paludosa* and *C. mollis* migrated from the Altai region into northern Europe and then spread west and south (see pp. 137, 139) and would therefore be referred to the Eurosiberian element. Of the other three species, *C. albida* is placed in the Mediterranean-montane element; whereas *C. lapsanoides* and *C. conyzaeifolia* are referred to the Aralo-Caspian element. Nevertheless, the synthesis of evidence on this genus shows conclusively that all three of these species must have migrated from western Asia by way of the Irano-Pontic-Balkan route (see pp. 140, 141).

Considering next a region far to the east, Korovin (1935) reports on the analysis of the present flora of Betpak-dala from the standpoint of its developmental history. This region is discussed here because the presence there of two fairly primitive species certainly indicates that the uplands were populated by *Crepis* in earlier times. *Crepis orcadensis* of section 11 is reported by Pavlov (1938, p. 368) to occur in the Ulutavsk (Ulu-Tau) Mountains near the Aral Sea, and in the mountains of southern Kazakstan, north of Lake Balkash. This Central Asiatic endemic is also fairly common in the mountains from Altai to Pamir. *Crepis pannonica* of section 10 is found on the steppes of Turgai, close to Betpak-dala, and in the mountains of northwestern Persia. Two of the most primitive species in this section, *C. darvasica* and *C. songorica*, are endemic in certain mountains of Russian Turkestan (cf. fig. 10, 10-DA, 10-AT).

The desert of Betpak-dala is that part of northern Turkestan lying between the

Sary-Su River on the west and Lake Balkash on the east. It is part of the vast Kirghiz steppe region which also includes the Turgai province to the northwest. The more mountainous Semipalatinsk region to the northeast merges into the Altai mountain region on the east. Korovin states that in southern Betpak-dala the flora is characterized by young species of the Mediterranean element. But most of the region, like the other northern deserts of Central Asia, has a flora characterized by primitive types, the Kirghiz element. Species belonging to this element occur in Ust-Urt (between the Caspian and Aral seas), in northern Turgai, in Betpak-dala, around Lake Balkash, in the central Tien Shan Mountains, and in the Pamir-Alai Mountains. It has been shown by Nalivkin (1926) that late in the Mesozoic era this region was composed of isolated massifs like the Ural and the central Tien Shan. In Miocene time there had been added the plateaus of Ust-Urt, Betpak-dala, and Turgai. The earliest fossil traces of the Kirghiz element are associated with the uplift of the mountains in the Miocene.

The Kirghiz element, according to Korovin, was derived from two different sources. Some of the species are relics of the old African or Gondwana flora which reached the Kirghiz region during the Cretaceous epoch. The other source of the Kirghiz element was Central Asia (which includes the Tien Shan–Altai region). This evidence that the present xerophytic flora of the Kirghiz steppes was derived in part from the middle Asiatic source supports the thesis that in mid-Tertiary times there was a westward and southwestward trend of plant migration from the Tien Shan–Altai region.

Turning now to Asia Minor, we find that Schwarz (1938), in his extensive review of the literature bearing more or less definitely on the floristic history of this region, reaches some generalizations which are of marked significance in connection with the southwestward migration of *Crepis* from Central Asia. After noting the striking picture made by the flora of Asia Minor, with its accumulation of distinct but closely related species, its unusually rich mosaic of vicariants, and its multiplicity of adaptive, progressive forms, he states that we make no mistake if we consider the Turco-Iranian primary flora as a distinct and continuous branch of the original flora of Angara continent, a branch which from the beginning won its direction by orientation to the continental climate. To the present author there appears to be no reason why *Crepis* should not be considered a part, or at least a derivative, of this original Angara flora.

Further, Schwarz also concludes that part of this primary flora migrated into the Iberian Peninsula and into the Atlas Mountains; and, since the traces of this invasion consist mostly of single species of the same genera or sections, with vicarious relatives in the primary development center, this extensive migration must have been relatively ancient. The Miocene is considered to be the epoch during which it occurred, and, incidentally, it is noted that the Dinaric (Dalmatian) Alps were probably uplifted in early Miocene. From the existence of related but highly divergent species of various genera in Central Asia and Asia Minor, Schwarz concludes that the Armenian-Kurdish mountain region formed a temporary distribution barrier with the consequent development of formenkreise in various groups. But it seems that the disturbance was not so prolonged and the isolation was not so great as to make a strongly marked secondary development center, because, as shown by the vertical distribution, the flora was relatively labile. A similar situation is seen in the overlapping of this primary flora in the mountains of the Aegean Islands and of Greece—its coherence, at least in the higher regions, was preserved. (These ideas are especially applicable to certain groups of *Crepis*; cf. sections 4, 6, 10, and 11.)

Schwarz also considers the peculiarities of the floras of northern and southern Asia Minor. The northern border of the region has a true relic flora and many of the types are now found in eastern Asia. Also, Asia Minor is definitely an area of refuge for the arctotertiary element in the sense of Engler. Southern and western Asia Minor has a true Mediterranean flora. At the same time, because of the many refuge areas extending from the western Himalayas to Makaronesia,¹ with relic species belonging to the primary flora, one can assume no outstanding secondary development center. To estimate the age of this Mediterranean-Sindic (Indian) refuge flora is very difficult. Certain of the trees, such as species of *Cedrus*, *Pinus*, and *Quercus*, appear in Eocene, Miocene, and Pliocene formations in Europe. *Since these trees and certain associated shrubs and herbs include Angara types, they must represent a definite west Eurasiatic development center for these elements in early Tertiary*; and this may be assumed to be the oldest Angiosperm stem of the Mediterranean flora. There are traces of this primary Mediterranean flora in Makaronesia.

According to Schwarz, the Dinaric connection between Europe and north Africa (Dalmatia, Italy, Sicily, Tunisia) had great significance for the preservation and spread of the west Eurasiatic Tertiary flora. Among the species that came in from western Asia is *Laurentia tenuella*, the present area of which, including Portugal, the Balearic Islands, Corsica, Sardinia, Sicily, Crete, Cyprus, and Liban, clearly marks the southern edge of the old Dinaric line, i.e., the original European-African contact zone, which dates probably from Pliocene time.

The immediate causes of decimation of the species comprising this primary (Angara) element of the Mediterranean flora are assumed by Schwarz to consist of rapid climatic changes which occurred in late Oligocene and early Miocene and again in late Pliocene and early Pleistocene (see also Handel-Mazzetti, 1909, p. 52). The elevation of the Dinaric range of the Alps provided new environments, especially for oreophytic types. Relic types from the old Tertiary western Eurasiatic primary flora also became fixed in the area north of the Alps (cf. *Crepis sibirica*). Furthermore, contacts were established during Miocene between the Mediterranean-Sindian, the Turco-Iranian, the old African, and the Euro-Sinic primary floras resulting in the Euro-Mediterranean secondary flora which was already well characterized in the Pliocene. This explains the presence of four *Cedrus* species in the Mediterranean area, the rich content of *Primula* section *Auricula* distributed from the Pyrenees to Bulgaria, and of section *Farinosa* from the Caucasus to the Balkan Peninsula, as it does also the presence of the primitive *P. frondosa*, etc.

Thus, we find that Engler's general hypothesis concerning the derivation of south European and Mediterranean relic species from Asiatic sources through a south-westerly migration trend from Central Asia is strongly supported by Schwarz's extensive review of the more recent literature in this field.

The comprehensive review of literature by Hagen (1914), which deals mainly with the floristic relations between the Mediterranean region in Africa and Asia, must be mentioned because of the significance of his conclusions concerning an important Tertiary plant migration southwesterly from Asia into the Mediterranean region. After reviewing the fossil Miocene-Pliocene flora of southern Europe, Hagen discusses the paleoclimate and floral history of the Sahara region. He concludes, with reference to climate in north Africa, that no prolonged desert conditions existed in the Sahara during Miocene-Pliocene; and even in the western part there was a generally moist climate. But the Pleistocene period brought extreme

¹ Makaronesia is a term used by several authors on vegetational history to designate the islands and archipelagoes of the eastern Atlantic—the Azores, Madeira, Canary, and Cape Verde Islands.

fluctuations. In Pluvial times, times corresponding to the Ice Age of alpine glaciation, the rainfall became so abundant that even in the western Sahara, during most of this period, many large rivers were formed. Also, corresponding with the longest interglacial period, a long drier period existed. In late Pleistocene and Recent times desiccation became gradually more pronounced.

With reference to floristic relations, it is noted that there are a few rather old species in both the Sahara and in Asia Minor which must be assumed to have had an Ethiopian origin. But there is a host of steppe and desert species in western and middle Asia which are represented in the Sahara by related species. The latter, according to Hagen, *must have originated in Asia, and one gets the impression that in earlier geologic times an actual wave of desert plants flowed from Asia into the Sahara and took possession of it.* Hagen also notes the existence of some peculiar endemics in the Sahara south of the Atlas Mountains, which probably had an early Mediterranean origin. But he considers almost all of the Saharan flora as Asiatic in origin. From a consideration of Tertiary-Pluvial relic species in north Africa, together with fossil evidence, our author concludes that there was a fairly broad littoral along the whole Mediterranean coast of north Africa during the Pluvial period, and south of this a steppe zone where all the Saharan xerophytic endemics could have been preserved. It is in this region that many of the advanced species of *Crepis* now occur, as well as several more primitive endemics.

Hagen next considers the relations between the floras of the Mediterranean-Near East region and the Ethiopian region. The rich endemic flora of Abyssinia consists of mesothermic species, some of which also occur on other high mountains in tropical Africa. In general, these endemics exhibit Mediterranean and Asiatic affinities. Engler's idea that such species "traveled by jumps," being borne by the wind or by birds, is accepted for these species, but it is emphasized that the route followed may have been partly over the sea. In this connection it may be noted that, according to Bailey Willis (oral communication), Africa was relatively flat until Middle Tertiary, when diversification began. From that time until mid-Pleistocene north Africa had for the most part a cool, moist climate. The latter part of the Tertiary would be the most likely period for the migration of *Crepis* from Asia to Africa. These species could have reached tropical Africa from southwestern Asia over either of two routes: (1) the Eritrean route, following the mountains of northern Persia, southern Asia Minor, Syria, the Sinai Peninsula, and a range of peaks along the Red Sea; (2) the south Arabian-Somaliland route, which can be traced from northwestern India, through Afghanistan, southeastern Persia, the border of southeastern Arabia, and Italian Somaliland. But from southern Arabia this route could have been through Eritrea, and this, with reference to the present distribution of *Crepis* in tropical Africa, seems more probable. In Pluvial times either of these routes must have been favorable.

Hagen also discusses the problem of floristic relations between the Mediterranean region and Makaronesia (the four groups of volcanic islands off the coast of north Africa). From the standpoint of *Crepis* history this is of minor importance and involves only the Canary and Madeira Archipelagoes. Hagen considers a former land connection of the Canary Islands with Morocco as good as proved, as he also does the contention that a former connection with Madeira Island existed (see also Willkomm, 1896, p. 260, cited by Handel-Mazzetti, 1909, p. 51). But his conclusion that the separation of both groups from the mainland occurred about the middle of the Tertiary period places that event too early for the rather advanced species of *Crepis* which are indigenous there to have migrated overland. There still remains the possibility, however, that they were transported by wind or birds.

The westerly trend from northern Central Asia.—The discovery of “a final link between the Tertiary floras of Asia and Europe” (Kryshtofovich, 1935) certainly indicates that the temperate deciduous flora of the Turgai province, moving westward around the southern end of the Ural Mountains, reached eastern Europe in late Oligocene or early Miocene time. During the Miocene period this temperate flora became dominant in Russia, which had formerly had the same tropical flora that extended from the Atlantic coast (cf. Reid and Chandler, 1933, p. 71) across Europe and southern Asia to the Indo-Malayan region, where it exists today. Evidence of the advent of the Turgayan Tertiary flora into eastern Russia was discovered near Sterlitamak, southwest of the Ural Mountains (about 54° N., and 56° E.). The fossil record is abundant and convincing. It may be taken to signify that the migration of the Turgayan flora into Europe south of the Ural Mountains, after desiccation of the Obic Sea along their eastern slope, was accompanied by the gradual displacement of the older tropical flora in eastern Europe. Concerning this important event in the history of the European flora, Chaney and Hu (*op. cit.*, p. 103) state: “The delayed arrival of the temperate flora as the dominant element in western Europe seems to have resulted from the continuous marine climate there into the Oligocene epoch. By Miocene time only remnants of the Tethys Sea appear to have remained and the vegetation had largely taken on the temperate aspect of the floras farther east in Eurasia, where continental climate had prevailed during most of the Tertiary period.” The establishment of this migration trend from Central Asia into Russia through the Turgai region and south of the Ural mountains sets an important precedent for the explanation of some aspects of the present distribution of *Crepis*.

The conception that angiospermous plants had their early development in Angara and that many members of that primitive flora migrated westward into Europe in Tertiary times has been accepted by other Russian botanists. V. P. Maleev (*in* Komarov, 1941, p. 143), for example, in discussing the Tertiary relic plants of western Transcaucasia, recognizes as one category *the mesophytic relics* of the “Angarida flora (A. N. Kryshtofovich’s ‘Turgai flora’) among which representatives of its northern and southern branches can be distinguished.” This allusion to the northern and southern branches of that part of the Angara flora which existed in Turgai can only mean that this author accepts two migration trends from the Turgai region, a westerly one and a southwesterly one. Maleev (*loc. cit.*) also accepts the view that this mesophytic flora was distributed throughout the whole Mediterranean region during Upper Pliocene and now persists only in the moister parts of that region. Similarly, J. D. Kleopov (*in* Komarov, 1941, p. 255) and M. M. Iljin (*op. cit.*, p. 292) both refer to Kryshtofovich’s Turgai flora which migrated into Europe in mid-Tertiary. This evidence of a wide acceptance of Kryshtofovich’s conclusions concerning the development of a temperate flora in northern Central Asia and the westward migration of many of its component species strengthens the foundation of our hypothetical history of *Crepis*.

SUMMARY

The general bearing of the foregoing review on the probable origin, development, and migrations of *Crepis* may be summarized as follows:

- 1) Ancient northern Asia, Angara Land, had been a relatively undisturbed continent for many millions of years previous to the Tertiary period.
- 2) The western part of the Altai-Tien Shan mountain region had been available since long before the Miocene epoch as a suitable region for the development of *Crepis* and its ancestors.

3) The fossil Tertiary floras of Asia and Europe indicate that in early Tertiary all of Europe except northern Russia and Scandinavia was tropical, whereas the northern half of Asia was temperate and became increasingly continental in character. Furthermore, the flora of the Turgai province, which includes the western Altai-Tien Shan region, indicates identical associations to those in which some *Crepis* species occur today.

4) By early Miocene the continents had risen sufficiently so that the Tethys Sea was greatly reduced, leaving two east-west arms on either side of a broad peninsula extending from southwestern Asia westward as far as Italy and eastern France. Also, the Obic Sea, separating Asia and Europe, had either disappeared or dried up sufficiently so that plant migration could occur south of the Ural Mountains.

5) During the last half of the Tertiary and the Quaternary period a great mountain axis extending from southeastern Asia to the Pyrenees was in process of elevation. Many new topographic conditions were interposed in the development of floras. At the same time, there was gradual desiccation of the region extending from Central Asia across the Mediterranean and northern Africa, accompanied by many relatively shorter fluctuations in moisture and temperature. All these changes were conducive to increased speciation in many genera, including *Crepis*.

6) During the Tertiary period there were four important trends of plant migration in Asia, all of which were significant for *Crepis*.

a) The northeasterly trend from Central Asia began at least as early as the Cretaceous period and continued throughout the Tertiary period. It was in the early part of this long period that such genera as *Fagus*, *Cedrus*, and *Datisca* probably migrated from Asia into North America. The American species of *Crepis*, or their ancestors, must have followed the same migration route in later Tertiary time.

b) The southeasterly trend from Central Asia began in early Tertiary, and by Middle Tertiary time *Dubyaea*, the ancestors of *Crepis*, and *Soroscris*, a nearly related genus, had probably migrated from Central to southeastern Asia.

c) The southwesterly trend from Central Asia into Europe and Africa also began, no doubt, before the Cenozoic era; but during the Tertiary period this trend of plant migration became increasingly important as a result of the general southward movement of vegetation in Asia. Evidence from various sources is found to show that there was a vast movement of plant species from Central Asia toward the southwest, with a profound effect on the floras of Europe and Africa, especially in the Mediterranean region. Many genera of flowering plants, including *Crepis*, were spread from Asia into both Europe and Africa during this long period. Even the high montane *Crepis* species of southern Europe, or their immediate ancestors, are believed to have migrated from Central Asia.

d) The westerly trend from Central Asia into northeastern Europe began in late Oligocene or early Miocene time. The present distribution of some of the most widespread *Crepis* species is explained by this migration trend.

CHAPTER 7

ENDEMISM IN THE OLD WORLD SPECIES OF *CREPIS*

THE DATA ON ENDEMISM IN *CREPIS*

SINCE THE TWELVE indigenous *Crepis* species of North America are all more or less widespread, they will not be included in this discussion of endemism in *Crepis*. It should be noted, however, that in each of the four most primitive American species there exists a 22-chromosome "diploid form" which has a narrow distribution and may properly be considered as endemic. From this and other evidence presented in detail in the monograph on the American species (Babcock and Stebbins, 1938), the conclusion was reached that all of the American species either migrated from Asia across the Beringian land bridge or were derived from Asiatic species which followed that route of migration in preglacial time.

From the evidence on geographic distribution which has been reviewed in the preceding chapters, it is clear that a Central Asiatic origin is indicated for this genus. In the course of this discussion reference was made to a number of endemic species. In the present chapter the data on restriction of distribution in the Old World species are examined for the purpose of determining the extent and significance of endemism for the history of the genus.

The term endemic, in its usual biological connotation, is applied to a plant or animal which is limited in its distribution to a single country, region, or area. Of equal or perhaps greater importance is the extent of the organism's actual range of distribution within the endemic area. In order to obtain more definite information concerning the amount and possible significance of endemism in *Crepis*, arbitrary limits were chosen. The upper limit was suggested by the fact that the primitive, relic species, *C. geracioides*, is known from three localities which are separated by a maximum distance of approximately 150 kilometers (94 miles). The lower limit (50 kilometers or 31 miles) was found to be sufficient to include the area occupied by such a local relic as *C. kilimandscharica*. In the classification of the endemic species, the term "narrow" was used when the maximum straight-line distance between the known localities of a species fell within the lower limit; when the maximum distance between the known localities exceeded the upper limit, the designation was "wider"; when the maximum distance fell between the two limits, those species were classed as "narrow B." It was found that there were so few species in the "narrow B" group that, for the sake of simplicity, the "narrow B" and "wider" groups were lumped together, thus recognizing only two categories, "narrow" and "wider," with the dividing line at 50 kilometers.

On this basis it was found that there are forty-eight species of *Crepis* for which the available data indicate a "narrow" distribution. Twenty-eight of these are known from only one locality, and the other twenty are known from two or more localities. Of the twenty-eight that are known from a single locality, twenty-four are known to the writer from just one collection; but the other four are known to have been collected several times at the one locality. Three of these four localities are mountain peaks in Greece; the other is the eastern promontory of Madeira Island. The twenty-four localities at which only a single collection has been made are mostly in regions which have been less thoroughly explored botanically, such as Asia Minor, the Caucasus, Turkestan, and tropical Africa. Many of these localities are in mountainous country and some are mountain peaks. Since many of the "wider" endemics are known to be very local in their distribution, and half of the "narrow" ones are known from two or more collections, it is fairly probable

that most of the species known from only one collection will turn out eventually to be, as here defined, actually "narrow." At any rate, the purposes of the present discussion can be better served by recognizing them as "narrow" than by ignoring them.

Classification of the rest of the *Crepis* species as endemic or not endemic was accomplished by defining a series of endemic areas and then by accepting as endemic only those known to be restricted to a single area. Many of these areas are widely recognized as rich in endemic species of plants. By this method 91 species were selected as "wider" endemics. This does not mean that these species are continuously distributed over a district more than 150 kilometers in diameter. On the contrary, these "wider" endemics are all more or less local in their distribution, even though a few are fairly abundant in certain districts. Thus, in *C. geracioides*, it happens that the three known localities are about 150 kilometers distant from one another; whereas *C. terglouensis*, another very primitive endemic, is known from at least twenty high alpine stations ranging from south-central Switzerland to central Tirol and Upper Austria, a distance of at least 350 kilometers. In marked contrast with these are such insular species as *C. cretica* and *C. canariensis*, which are abundant on the islands where they exist. A few species have been omitted which occur mostly in one endemic area but are also represented in another and hence, on a less restricted criterion, might have been considered as endemic. Interesting examples are *C. pygmaea*, a very primitive 12-chromosome species of Spain, the Pyrenees, the southwestern Alps, and northern Italy; *C. smyrnaea*, another 12-chromosome primitive species known from only three localities in southern Greece and western Asia Minor; *C. pontana*, the most primitive 10-chromosome species of *Crepis*, which occurs from the eastern Alps to the western part of the Balkan Peninsula; and *C. albida*, the next most primitive 10-chromosome species, which is polymorphic and is distributed from the Grand Atlas Mountains, in Morocco through Spain, the mountains of southern France, and the Maritime Alps. It becomes difficult to determine where to draw the line if one begins to go beyond the limits of a single endemic area. But on this restricted basis there are still 133 endemic species, which is 72 per cent of the 185 Old World species.

These 133 species, together with section numbers, are listed on the left-hand pages of table 8. Other pertinent data are, in order, as follows: the endemic region (Roman numerals); the endemic area (Arabic numerals); the number of localities at which it is known to have been collected; its distribution class (as determined from map measurements of maximum distance between known localities); and the serial number. On the facing right-hand pages are given the serial number; the phylogenetic group of each species (whether most primitive [primitive A], less primitive [primitive B], intermediate, or advanced); its altitude class (alpine, montane, or low); its moisture classification (as occupying a moist, subhumid, or arid environment); its life-duration class (perennial or annual-biennial); its variability class (monomorphic or polymorphic); and, finally, its diploid chromosome number when that is known. (Only three of the species are polyploids, and in these the chromosome number, shown in italics, is the basic, not the diploid number.) By means of this system of classification it has been possible to derive some significant generalizations concerning the relations between phylogeny and endemism in *Crepis*. Before considering these relations, however, let us examine the distribution of the endemic regions and areas.

The distribution of the endemic regions and areas for Crepis.—The endemic regions and areas for *Crepis* are defined in table 9 and shown in figure 10. In this figure the large size of the tropical African area (no. 19) will be one of the first

TABLE 8
THE ENDEMIC SPECIES OF CREPIS OF THE OLD WORLD

Section	Species	Region	Area	Number of localities known	Distribution class	Serial number
1	<i>C. geracioides</i> ...	II	4	3	narrow B	1
1	<i>C. viscidula</i>	II	4	20+	wider	2
2	<i>C. kashmirica</i>	VI	11-HI	10	wider	3
4	<i>C. terglouensis</i>	I	3	20	wider	4
4	<i>C. rhaetica</i>	I	3	20+	wider	5
4	<i>C. hokkaidoensis</i>	IX	15-i, j	10	wider	6
4	<i>C. albiflora</i>	III	5-KD	1	narrow A	7
4	<i>C. dioritica</i>	III	5-CT	2	narrow A	8
5	<i>C. lapsanoides</i>	I	2	12	wider	9
5	<i>C. willemetioides</i> ..	IV	9-AK	2	narrow B	10
5	<i>C. hierosolymitana</i>	III	6	14	wider	11
5	<i>C. montana</i> ..	II	4-Greece	13	wider	12
5	<i>C. Mungierii</i>	II	4-c, k	7	wider	13
7	<i>C. achyrophoroides</i>	X	18	2	narrow A ?	14
7	<i>C. elymatica</i>	IV	9-KS	2	wider	15
8	<i>C. kilimandscharica</i>	XI	19-KI	5	narrow A	16
8	<i>C. keniensis</i> ..	XI	19-KE	2	narrow A	17
8	<i>C. suffruticosa</i>	XI	19-ME	1	narrow A	18
8	<i>C. iringensis</i>	XI	19-RM	2	narrow A	19
8	<i>C. meruensis</i>	XI	19-Me, KI	5	narrow B	20
8	<i>C. cameroonica</i>	XI	19-MC	5	narrow A	21
8	<i>C. Schultzii</i>	X	18	3	narrow A ?	22
8	<i>C. urundica</i>	XI	19-UK	1	narrow A	23
8	<i>C. chirindica</i>	XI	19-CH	1	narrow A	24
8	<i>C. congoensis</i>	XI	19-EC	1	narrow A	25
8	<i>C. caudicalis</i>	XI	19-MC ?	2	narrow A	26
8	<i>C. glandulosissima</i>	XI	19-KE +	2	wider	27
8	<i>C. ugandensis</i>	XI	19-FU	1	narrow A	28
8	<i>C. Swynnertonii</i>	XI	19-NY	6	wider	29
8	<i>C. subscaposa</i>	VII	13	6	wider	30
8	<i>C. simulans</i>	XI	19-CH	1	narrow A	31
8	<i>C. Gossweileri</i>	XI	19-CA	1	narrow A	32
8	<i>C. Freisii</i>	XI	19-KU	1	narrow A	33
8	<i>C. Mildbraedii</i>	XI	19-CU	2-3	wider	34
8	<i>C. Bruceae</i>	XI	19-UL	1	narrow A	35
9	<i>C. tingitana</i>	I	1	16	wider	36
9	<i>C. leontodontoides</i>	XII	23	many	wider	37
9	<i>C. suberostris</i>	XII	24	8	wider	38
10	<i>C. Strausii</i>	IV	9-PS	3	narrow B ?	39
10	<i>C. darvasica</i>	V	10-DA	1	narrow A	40
10	<i>C. songorica</i>	V	10-AT	5	wider ?	41
10	<i>C. sonchifolia</i>	IV	8	2	narrow A ?	42
10	<i>C. ciliata</i> ..	IV	8	4	wider	43
10	<i>C. latialis</i> ...	XII	23	13+	wider	44
10	<i>C. bertisceae</i>	II	4	1	narrow A	45
10	<i>C. chondrilloides</i>	II	4	many	wider	46
10	<i>C. bupleurifolia</i> ..	III	5	3	wider	47
10	<i>C. auriculaefolia</i>	II	4-c	9	wider	48
10	<i>C. Baldaccii</i>	II	4	4	wider	49

TABLE 8
THE ENDEMIC SPECIES OF CREPIS OF THE OLD WORLD

Serial number	Phylogenetic group	Altitude class	Moisture class	Duration class	Variability class	Basic chromosome number
1	primitive A	montane	subhumid	perennial	monomorphic	6
2	primitive A	alpine	moist	perennial	monomorphic	6
3	primitive A	alpine	subhumid	perennial	monomorphic	6
4	primitive A	alpine	subhumid	perennial	monomorphic	6
5	primitive A	alpine	subhumid	perennial	monomorphic	—
6	primitive A	alpine	subhumid	perennial	monomorphic	4
7	intermediate	alpine	subhumid ?	perennial	monomorphic	4
8	intermediate	alpine	subhumid ?	perennial	monomorphic	—
9	primitive A	montane	moist	perennial	monomorphic	6
10	primitive B	low ?	arid ?	perennial	monomorphic	6
11	intermediate	low	arid	perennial	monomorphic	6
12	intermediate	low	arid	perennial	polymorphic	6
13	intermediate	montane	arid	perennial	polymorphic	6
14	primitive B	montane	subhumid	perennial	monomorphic	—
15	intermediate	montane	arid ?	perennial	monomorphic	—
16	primitive A	montane	moist	perennial	monomorphic	4
17	primitive A	montane	moist	perennial	monomorphic	—
18	primitive A	alpine	subhumid	perennial	monomorphic	4
19	primitive A	montane	subhumid	perennial	monomorphic	—
20	primitive A	montane	subhumid	perennial	polymorphic	—
21	primitive A	montane	subhumid	perennial	monomorphic	—
22	primitive B	montane	moist	perennial	monomorphic	—
23	primitive B	montane	moist	perennial	monomorphic	—
24	intermediate	montane	subhumid	perennial	monomorphic	—
25	intermediate	low	subhumid	perennial	monomorphic	—
26	intermediate	low	subhumid	perennial	monomorphic	—
27	intermediate	montane	subhumid	perennial	monomorphic	—
28	intermediate	low	subhumid	perennial	monomorphic	—
29	intermediate	low	subhumid	perennial	polymorphic	—
30	intermediate	montane	moist	perennial	monomorphic	—
31	intermediate	montane	subhumid	perennial	monomorphic	—
32	intermediate	low	moist	perennial	monomorphic	—
33	intermediate	montane	subhumid	perennial	monomorphic	—
34	intermediate	low	subhumid	perennial	monomorphic	—
35	intermediate	montane	subhumid	perennial	monomorphic	—
36	primitive B	low	arid	perennial	polymorphic	5
37	intermediate	low	arid	perennial	polymorphic	5
38	advanced	low	arid	annual	polymorphic	5
39	primitive B	montane	subhumid ?	perennial	monomorphic	—
40	primitive B	montane	subhumid	perennial	monomorphic	—
41	primitive B	montane	subhumid	perennial	monomorphic	—
42	primitive B	low	subhumid	perennial	monomorphic	—
43	primitive B	low	subhumid	perennial	monomorphic	5
44	intermediate	low	subhumid	perennial	polymorphic	4
45	intermediate	montane	arid ?	perennial	monomorphic	—
46	intermediate	low	subhumid	perennial	monomorphic	4
47	intermediate	montane	subhumid	perennial	polymorphic	—
48	primitive B	montane	arid	perennial	monomorphic	—
49	primitive B	montane	subhumid	perennial	monomorphic	5

TABLE 8—(Continued)

Section	Species	Region	Area	Number of localities known	Distribution class	Serial number
10	<i>C. turcica</i> ...	II	4	4	narrow B	50
10	<i>C. Pantocsekii</i>	II	4	6	wider	51
10	<i>C. Triasii</i> ...	I	1-a	many	narrow B	52
10	<i>C. Raulini</i>	II	4-c	3	narrow B	53
10	<i>C. albanica</i>	II	4-NA	2	narrow A	54
10	<i>C. macropus</i>	III	5	8	wider	55
10	<i>C. oporinoides</i>	I	1	18	wider	56
10	<i>C. dens-leonis</i>	IV	8-CA	1 or 2	narrow A ?	57
10	<i>C. Sibthorpiana</i>	II	4-c	2	narrow B	58
10	<i>C. khorassanica</i>	IV	9-KN	1	narrow A	59
10	<i>C. incana</i>	II	4	5	wider	60
10	<i>C. taygetica</i>	II	4-TA	1	narrow A	61
10	<i>C. turcomanica</i>	IV	9-AC	2	narrow A ?	62
10	<i>C. Guioliana</i> ...	II	4-MS	1	narrow A	63
10	<i>C. crocifolia</i>	II	4-TA	1	narrow A	64
10	<i>C. athoa</i> ...	II	4-AO	1	narrow A	65
11	<i>C. Schachtii</i>	II	4-AB	1	narrow A	66
11	<i>C. pinnatifida</i>	III	5	3-5	wider	67
11	<i>C. oreades</i> ...	V	10-UT, P-A	12+	wider	68
11	<i>C. tencrrima</i>	X	18-SM	1	narrow A	69
11	<i>C. xylorrhiza</i> ...	X	18-SM	2	narrow A	70
11	<i>C. Hookeriana</i>	I	1-GA	7	wider	71
11	<i>C. Faureliana</i>	I	1-SA	1	narrow A	72
11	<i>C. Robertioides</i>	III	6-II, AL	17	narrow B	73
11	<i>C. heterotricha</i>	IV	9	5	wider	74
11	<i>C. armena</i> ...	III	5	5	wider	75
11	<i>C. demavendi</i>	IV	9-EL	1	narrow A	76
11	<i>C. abyssinica</i>	X	18	2	narrow A ?	77
12	<i>C. corniculata</i>	V	10-P, AI, TI	7	wider	78
12	<i>C. alaica</i> ...	V	10-AI, TI	4	narrow B	79
12	<i>C. naniforma</i>	VI	11-HI	3	wider	80
12	<i>C. lactea</i> ...	V	10-P, TS	6	wider	81
13	<i>C. gymnopus</i>	IX	15-i	4	wider	82
16	<i>C. connexa</i>	IV	9-SV	2	narrow B ?	83
16	<i>C. sahendi</i>	IV	8	6	wider	84
16	<i>C. purpurea</i>	III	7	3	narrow B	85
16	<i>C. elbrusensis</i>	IV	9-EL	3	narrow B	86
16	<i>C. frigida</i> ...	III	5	4	wider	87
17	<i>C. napifera</i> ...	VII	13	12	wider	88
18	<i>C. Phoenix</i> ...	VII	13	5+	wider	89
18	<i>C. Bodinieri</i>	VII	13	10	wider	90
18	<i>C. rigescens</i>	VII	13	17	wider	91
18	<i>C. lignea</i>	VII	13	14	wider	92
18	<i>C. chloroclada</i>	VII	13-SH	1	narrow A	93
19	<i>C. palaestina</i>	III	6	10	wider	94
19	<i>C. amanica</i>	III	6-DU	1	narrow A	95
19	<i>C. Stojanovi</i> ...	II	4	4	narrow B	96
19	<i>C. pterothecoides</i>	III	6-AL, etc.	4	narrow B	97
20	<i>C. syriaca</i> ...	III	6	13	wider	98

TABLE 8—(Continued)

Serial number	Phylogenetic group	Altitude class	Moisture class	Duration class	Variability class	Basic chromosome number
50	intermediate	montane	subhumid	perennial	polymorphic	—
51	intermediate	montane	subhumid	perennial	monomorphic	—
52	intermediate	low	arid	perennial	monomorphic	4
53	intermediate	alpine	subhumid	perennial	monomorphic	5
54	intermediate	montane	subhumid	perennial	monomorphic	—
55	intermediate	low	arid	perennial	monomorphic	—
56	intermediate	montane	subhumid	perennial	polymorphic	4
57	intermediate	montane	subhumid ?	perennial	monomorphic	—
58	intermediate	alpine	subhumid	perennial	monomorphic	—
59	intermediate	alpine	subhumid	perennial	monomorphic	—
60	intermediate	montane	subhumid	perennial	monomorphic	4
61	intermediate	alpine	subhumid	perennial	monomorphic	5
62	intermediate	montane	subhumid	perennial	monomorphic	—
63	intermediate	montane	subhumid ?	perennial	monomorphic	—
64	intermediate	alpine	subhumid	perennial	monomorphic	—
65	intermediate	alpine	subhumid	perennial	monomorphic	—
66	primitive B	montane	arid	perennial	monomorphic	5
67	intermediate	alpine	subhumid	perennial	monomorphic	—
68	primitive B	montane	arid	perennial	polymorphic	4
69	intermediate	montane	moist	perennial	monomorphic	—
70	intermediate	alpine	moist	perennial	monomorphic	—
71	primitive B	alpine	subhumid	perennial	monomorphic	4
72	intermediate	montane	arid	perennial	monomorphic	—
73	intermediate	alpine	moist	perennial	monomorphic	4
74	intermediate	alpine	subhumid	perennial	polymorphic	—
75	intermediate	alpine	subhumid	perennial	polymorphic	—
76	intermediate	alpine	moist ?	perennial	monomorphic	—
77	intermediate	alpine	arid ?	perennial	monomorphic	—
78	intermediate	alpine	moist ?	perennial	monomorphic	—
79	intermediate	alpine	moist	perennial	monomorphic	—
80	intermediate	alpine	moist	perennial	monomorphic	—
81	intermediate	alpine	moist	perennial	monomorphic	—
82	intermediate	alpine	moist ?	perennial	monomorphic	4
83	primitive B	montane	subhumid	perennial	monomorphic	—
84	intermediate	alpine	subhumid	perennial	monomorphic	—
85	intermediate	low	subhumid	perennial	monomorphic	—
86	intermediate	alpine	subhumid	perennial	monomorphic	—
87	intermediate	alpine	subhumid	perennial	monomorphic	—
88	intermediate	montane	subhumid	perennial	monomorphic	—
89	intermediate	montane	subhumid	perennial	polymorphic	—
90	intermediate	montane	subhumid ?	perennial	polymorphic	—
91	intermediate	montane	arid ?	perennial	polymorphic	—
92	intermediate	montane	arid	perennial	polymorphic	—
93	intermediate	montane	arid	perennial	monomorphic	—
94	advanced	low	subhumid	annual	polymorphic	4
95	advanced	montane	subhumid ?	annual	monomorphic	—
96	advanced	low	arid	annual	monomorphic	4
97	advanced	montane	arid	annual	polymorphic	4
98	advanced	low	arid	annual	polymorphic	5 (+)

TABLE 8—(Concluded)

Section	Species	Region	Area	Number of localities known	Distribution class	Serial number
20	<i>C. Schimperii</i> ..	X	18	6	wider	99
20	<i>C. eritreënsis</i> .	X	17	5	narrow A	100
20	<i>C. Thomsonii</i> .	VI	12	16	wider	101
20	<i>C. tybakiensis</i>	II	4-c	1	narrow A	102
21	<i>C. tibetica</i> .	VII	13	5	wider	103
21	<i>C. Gmelini</i> .	VIII	14	2	wider	104
21	<i>C. elongata</i>	VII	13	4	wider	105
23	<i>C. patula</i>	XII	22	7	wider	106
23	<i>C. Dioscoridis</i> .	II	4-Greece	many	wider	107
23	<i>C. multiflora</i> ..	II	4-Aegean	20+	wider	108
24	<i>C. insignis</i> ...	III	6	1	narrow A	109
24	<i>C. corymbosa</i> .	XII	23-Italy, h	8	wider	110
24	<i>C. fuliginosa</i> ..	II	4-Greece	many	wider	111
24	<i>C. cretica</i> ..	II	4-c	many	wider	112
24	<i>C. apula</i> ..	XII	23-Italy	3	wider	113
24	<i>C. Suffreniana</i> .	XII	23-France	10	wider	114
25	<i>C. spathulata</i> .	XII	23-b	10 ?	wider	115
25	<i>C. Salzmannii</i>	XII	24	5	wider	116
25	<i>C. Fontiana</i> ..	XII	24	2	narrow B	117
25	<i>C. Bourgeaui</i> .	XII	24	4	narrow B ?	118
25	<i>C. canariensis</i>	XII	25-g	many	narrow B	119
25	<i>C. divaricata</i> .	XII	25-e	1	narrow A	120
25	<i>C. Noronhaea</i> .	XII	25-f	6	narrow A	121
25	<i>C. Balliana</i> ..	XII	24	1	narrow A	122
25	<i>C. libyca</i> .	XII	20	9	wider	123
25	<i>C. Claryi</i>	XII	24-SA	2	narrow A	124
26	<i>C. juvenalis</i> .	XII	21	6	wider	125
26	<i>C. aculeata</i> .	III	6	9	wider	126
26	<i>C. atheniensis</i>	II	4-Greece	1	narrow A	127
26	<i>C. aspera</i> ..	III	6	19	wider	128
26	<i>C. Muhlisii</i>	III	5	2	narrow A	129
27	<i>C. Forskalii</i> ..	X	16	2	narrow A	130
27	<i>C. bellidifolia</i> ..	XII	24-a, d	many	wider	131
27	<i>C. bursifolia</i>	XII	24-Italy, b	12	wider	132
27	<i>C. filiformis</i>	XII	20	2	narrow A ?	133

TABLE 8—(Concluded)

Serial number	Phylogenetic group	Altitude class	Moisture class	Duration class	Variability class	Basic chromosome number
99	advanced	montane	arid	annual	monomorphic	—
100	advanced	montane	subhumid	annual	monomorphic	5
101	advanced	montane	arid ?	annual	polymorphic	5
102	advanced	low	arid	annual	monomorphic	—
103	intermediate	alpine	subhumid ?	perennial	polymorphic	—
104	intermediate	montane	subhumid	perennial	monomorphic	—
105	intermediate	montane	subhumid	perennial	monomorphic	—
106	intermediate	low	moist	perennial	monomorphic	4
107	advanced	low	arid	annual	polymorphic	4
108	advanced	low	arid	annual	polymorphic	4
109	advanced	low	arid	annual	monomorphic	—
110	advanced	low	arid	annual	polymorphic	4
111	advanced	montane	arid	annual	polymorphic	3
112	advanced	montane	arid	annual	monomorphic	4
113	advanced	low	arid	annual	monomorphic	4
114	advanced	low	arid	annual	monomorphic	4
115	intermediate	low ?	arid	perennial	monomorphic	—
116	intermediate	low	arid	perennial	monomorphic	—
117	intermediate	low	subhumid	perennial	monomorphic	4
118	intermediate	low	subhumid	perennial	monomorphic	4
119	intermediate	low	arid	perennial	monomorphic	4
120	intermediate	low	subhumid	perennial	monomorphic	4
121	intermediate	low	arid	perennial	monomorphic	4
122	intermediate	low	subhumid	perennial ?	monomorphic	—
123	advanced	low	arid	perennial	monomorphic	4
124	advanced	montane	arid	annual	monomorphic	—
125	advanced	low	arid	annual	polymorphic	4
126	advanced	low	arid	annual	monomorphic	4
127	advanced	low	arid	annual	monomorphic	—
128	advanced	low	arid	annual	polymorphic	4
129	advanced	low	arid	annual	monomorphic	—
130	advanced	montane	subhumid	perennial	monomorphic	—
131	advanced	montane	subhumid	perennial	polymorphic	4
132	advanced	low	subhumid	perennial	monomorphic	4
133	advanced	low	arid	annual	monomorphic	—

TABLE 9
 ENDEMIC REGIONS AND AREAS FOR OLD WORLD CREPIS

<i>Regions</i>	<i>Areas</i>
I. Southwestern Europe; Alps; north-western Morocco.....	1. S. Spain and N. W. Morocco 2. N. E. Spain and W. France 3. European Alps
II. Balkan Peninsula.....	4. Balkan Peninsula
III. Asia Minor; Syria-Palestine; Crimea...	5. Asia Minor 6. Syria and Palestine 7. Crimea
IV. Caucasus; Iran.....	8. Caucasus region 9. Iran
V. Turkestan-Pamir-Altai region....	10. Turkestan, i. e., E. and N. Russian Turkestan and the Pamir-Altai Mountains
VI. Northwestern India ...	11. N. W. Himalaya Mountains, high alpine 12. N. W. India-Baluchistan, low montane
VII. Southeastern Asia ...	13. S. E. Asia (= S. E. Tibet, S. W. China, N. Burma, Laos, Annam)
VIII. Eastern Siberia .	14. E. Siberia (Okhotsk district)
IX. Northern Japan	15. Hokkaido-Sakhalin
X. Abyssinia; Eritrea; southwestern Arabia	16. S. W. Arabia (in Yemen Province) 17. Eritrea 18. N. Abyssinia, mountains
XI. Africa, tropical	19. Africa, tropical (isolated localities)
XII. Lybia-Morocco-Cadiz (littoral); southern and western maritime Italy and southern France; Madeira and Canary Islands.....	20. Lybia (littoral) 21. Tunisia (middle and southern) 22. E. Algeria (littoral) 23. S. Italy and Toscana, Sicily, Sardinia, Corsica; S. France 24. W. Algeria, N. Morocco, Cadiz (mostly littoral) 25. Madeira and Canary Islands

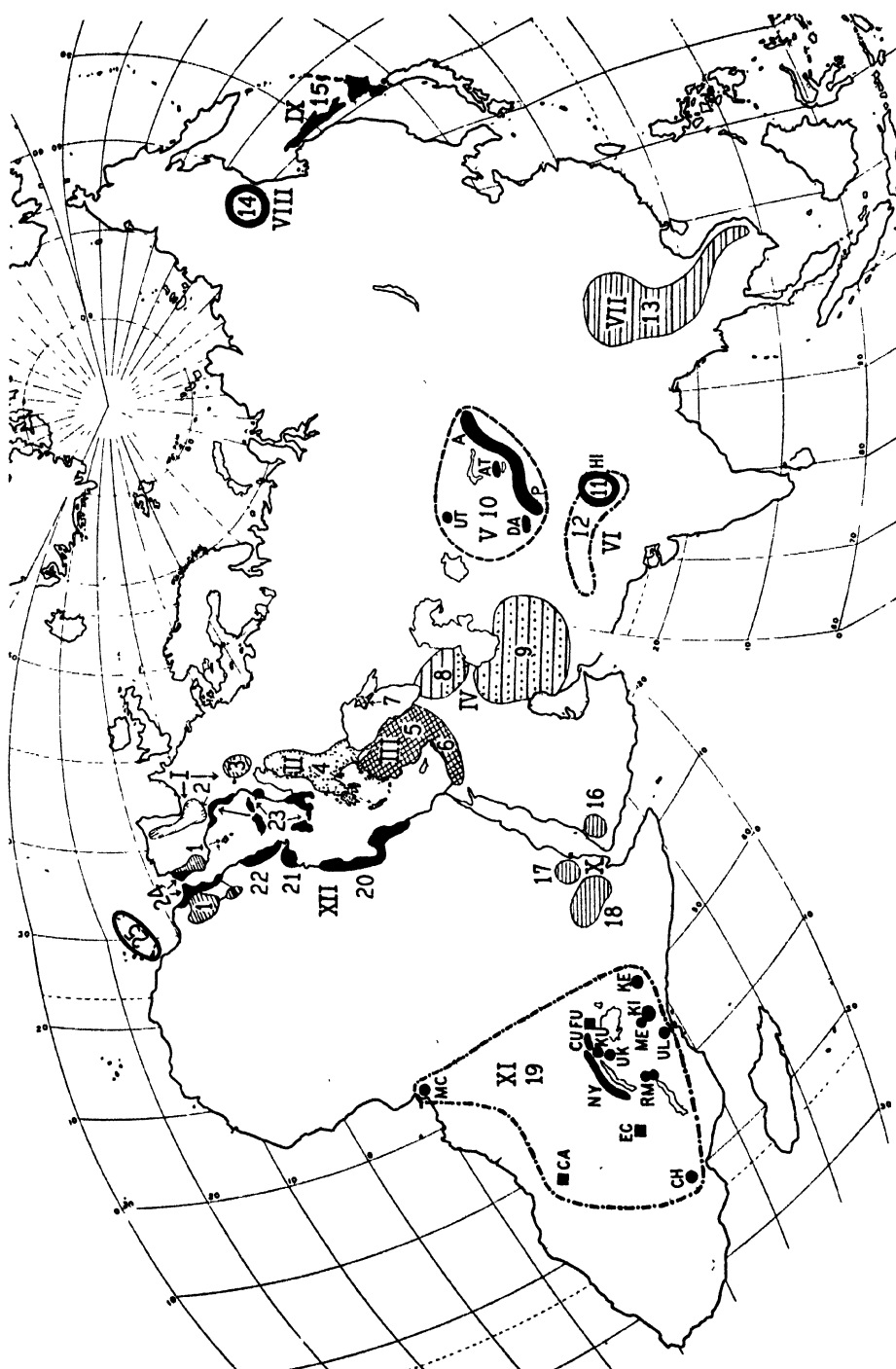


Fig. 10. Map of the Old World, showing the location and approximate size of all the endemic regions (indicated by Roman numerals) and areas (Arabic numerals) for *Crepis*. See tables 8 and 9. Based on Goode *Base Map No. 201 PC*. By permission of the University of Chicago Press.

things to catch the attention. It should be emphasized that all of the eighteen endemic species found in this area are extremely local in distribution. All but three, from the data now available, occur on only one or two mountains or in a single mountain range. These mountains and ranges are shown as solid circles or narrow ellipses. The other three species, shown as solid squares, are known from single stations which are at low elevation. The key to the symbols used to designate endemic localities in table 8, some of which symbols are also used in areas 10 and 19 in figure 10, are as follows:

INDIVIDUAL MOUNTAINS OR RANGES OF MOUNTAINS

- AB. Mt. Ali Botusch, eastern Macedonia, Bulgaria.
- AC. Achal-Tekke Mts., southwestern Turkestan (area 9, region IV).
- AI. Alai Mts., Ferghana, eastern Russian Turkestan.
- AK. Alla-Dagh and Kopet-Dagh, northeastern Iran.
- AL. Anti-Liban Mts., southwestern Syria.
- AO. Mt. Athos, Hagion Oros Peninsula, Greece.
- AT. Ala-Tau Mts., Central Asia.
- CA. Caucasus Mts.
- CH. Mt. Chirinda, southeastern Africa.
- CT. Cilician Taurus, southern Asia Minor.
- DA. Darvas Mts., eastern Russian Turkestan.
- DU. Mt. Dumanly, Amanus Mts., northern Syria.
- CU. Congo-Uganda plateau north of Lake Kiwu, tropical Africa.
- EL. Elburz Mts., northern Iran.
- GA. Great Atlas Mts., Morocco.
- HI. Himalaya Mts., Kashmir, high alpine.
- KD. Kop-Dagh, western Armenia.
- KE. Mt. Kenya, eastern tropical Africa.
- KI. Mt. Kilimanjaro, eastern tropical Africa.
- KN. Kuh-i-Nishapur Mts., northeastern Iran.
- KS. Kuh-i-Gerru and Schuturun Mts., western Iran.
- KU. Mountains south of Lake Kiwu, tropical Africa.
- LI. Liban Mts., southwestern Syria.
- MC. Mt. Cameroon, western tropical Africa.
- ME. Mt. Meru, eastern tropical Africa.
- MS. Mt. Smolika, western Greece.
- NA. North Albanian Alps.
- NY. Mountains of Nyasaland, extending into Belgian Congo, Africa.
- P. Pamir Mts., southern Central Asia.
- P-A. Pamir-Altai mountain system.
- PS. Kuh-i-Parrau and Mt. Shahu, western Iran.
- RM. Mt. Rungwe and Mt. Mbeya, tropical Africa.
- SA. Saharan Atlas, southern Algeria.
- SH. Shan Hills, eastern Burma.
- SM. Simen Mts., Amhara-Tigre Province, Abyssinia.
- SV. Shahu and Avroman Mts., western Iran.
- TA. Mt. Hagios Elias, Taygetos Mts., southwestern Greece.
- TI. Transalai Mts., Ferghana, eastern Russian Turkestan.
- TS. Tien Shan Mts., Central Asia.
- UK. Urundi Province, Kisozi, tropical Africa.
- UL. Uluguru Mts., Tanganyika Province, tropical Africa.
- UT. Ulu-Tau Mts., northern Russian Turkestan.

SINGLE LOWLAND STATIONS IN AFRICA

(Shown as solid squares in figure 10.)

- CA. Cului, Angola.
- EC. Elisabethville, southeastern Belgian Congo.
- FU. Fort Portal, Uganda.

INDIVIDUAL ISLANDS OR GROUPS OF ISLANDS

- a. Balearic (Majorca).
- b. Sicily.
- c. Crete.
- d. Corsica-Sardinia.
- e. Madeira.
- f. Porto Santo.
- g. Lanzarote, Fuerteventura.
- h. Corfu-Cephalonia.
- i. Hokkaido (or Yezo).
- j. Sakhalin.
- k. Karpathos.

The distribution of the twelve endemic regions defines the east-west distribution of the genus as a whole almost completely, the gaps between the endemic regions being occupied more or less by the various widespread species. In this connection it should be repeated that the total evidence on geographic distribution in *Crepis*, considered in relation to the evidence on phylogeny, definitely indicates that the center of origin and early development of *Crepis* was in Central Asia, in the Altai-Tien Shan mountain region in the northeastern part of region V (fig. 10); and that the present wide distribution of the genus was accomplished through migration from that center. One migration trend was to the east and northeast, resulting in the two endemics of Japan and the one in the Okhotsk district of Siberia (regions VIII and IX, fig. 10). Another trend was to the southeast, resulting in the nine endemic species found in region VII. Most important of all the migration trends from Central Asia, in terms of the number of species involved, was the south-westerly trend across Turkestan and Iran. From this region three branches led to northwestern and tropical Africa, to the Caucasus, Asia Minor, and southern Europe, and to the eastern Mediterranean and north African littoral. The point to be emphasized here is that the distribution of the endemic regions for *Crepis* is entirely consistent with the history of the genus as a whole.

PHYLOGENY AND ENDEMISM IN CREPIS

Based on the evidence from comparative morphology and cytogenetics, it has been possible to classify all the species of *Crepis* on a relative phylogenetic basis with some degree of assurance. For purposes of the present discussion they have been grouped into three classes, the more primitive, the intermediate, and the more advanced species. In table 10 are shown the relations of the endemic species in these phylogenetic groups to the size of area occupied by each species, to its altitude and moisture classification, and to its life-duration and variability.

Considering first the totals in the right-hand column, it will be noted that 29 of the endemic species are primitive and 29 are advanced, whereas 75, or more than one-half of them, are intermediate. The fact that *Crepis* may evidently be described as a conservative genus becomes more patent when it is realized that of the 29 advanced endemics only some half-dozen desert or montane annuals can be considered as very highly specialized species. Apparently no correlation exists between the phylogenetic grouping and extent of distribution (narrow *vs.* wider), since about one-third of all the endemics are narrow and two-thirds are wider, and these same proportions hold roughly for each of the three phylogenetic classes. In altitudinal distribution there is positive correlation between primitive type and alpine altitude and very strong positive correlation between advanced type and low altitude. In the moisture classes we find that, of the 104 endemics in the primitive and intermediate groups taken together, just one-fifth occur under arid conditions,

TABLE 10

RELATIONS BETWEEN THE PHYLOGENETIC GROUPS OF 133 ENDEMIC SPECIES OF CREPIS AND THEIR EXTENT OF NATURAL DISTRIBUTION, ELEVATION, GENERAL MOISTURE CONDITION, DURATION OF LIFE, AND VARIABILITY

Phylogenetic groups	Distribution classes		Altitude classes			Moisture classes			Duration classes		Variability classes		Totals
	Narrow	Wider	Alpine	Montane	Low	Moist	Subhumid	Arid	Perennial	Annual or biennial	Mono-morphic	Poly-morphic	
Primitive	11	18	7	18	4	6	18	5	29		26	3	29
Intermediate.	28	47	24	28	23	12	46	17	75		61	14	75
Advanced	9	20		10	19		6	23	4	25	17	12	29
Totals.	48	85	31	56	46	18	70	45	108	25	104	29	133

TABLE 11

RELATIONS OF THE HAPLOID CHROMOSOME NUMBERS 6, 5, 4, 3 TO THE PHYLOGENETIC GROUP, EXTENT OF NATURAL DISTRIBUTION, ELEVATION, MOISTURE, DURATION OF LIFE, AND VARIABILITY OF 52 ENDEMIC SPECIES OF CREPIS
(The polyploid endemics *C. ciliata*, *C. incana*, and *C. taygetica* are omitted)

Chromosome numbers	Phylogenetic groups			Distribution classes		Altitude classes			Moisture classes			Duration classes		Variability classes		Totals
	Primitive	Intermediate	Advanced	Narrow	Wider	Alpine	Montane	Low	Moist	Sub-humid	Arid	Perennial	Annual or biennial	Monomorphic	Polymorphic	
<i>n</i> = 6.	6	3			9	3	3	3	2	3	4	9		7	2	9
<i>n</i> = 5	3	2	4	2	7	1	4	4		3	6	5	4	4	5	9
<i>n</i> = 4.	5	13	15	6	27	6	4	23	5	14	14	21	12	22	11	33
<i>n</i> = 3...			1		1		1				1		1		1	1
Totals.....	14	18	20	8	44	10	12	30	7	20	25	35	17	33	19	52

One of these, the Abyssinian region, differs from the other four in having all the phyletic groups represented. The ten endemics of this region are all montane except the two primitive species, which are alpine; and, yet, four of these montane species are advanced. It will be recalled, however, that certain other advanced species are montane. This is true of the one 3-paired endemic, *C. fuliginosa*, which occurs in southern Greece, and of its 4-paired close relative, *C. cretica*. The three other regions contain only perennial endemics, none of which is advanced, some being intermediate and some primitive. Southwestern Europe and tropical Africa are important regions for the most primitive endemics, since nine of the twenty-six endemics found in those two regions are classed as primitive-A. Thus, at the western extremes of distribution for *Crepis*, we find the greatest concentration of the most primitive endemics in the genus.

In order to give another picture of the morphological contrasts between the most primitive and the most advanced species in the genus, *C. terglouensis*, an alpine endemic of the European Alps, is shown in fig. D, *a-f*, and *C. fuliginosa*, a lower montane endemic of Greece, in fig. D, *a'-f'*. The plants and their parts are drawn at comparable scales. It will be noted, also, that in their haploid sets of chromosomes, the two species represent the extremes of karyotype variation found in this genus.

With reference to the chromosomes of fifty-two of the endemic species (table 12), it is clear that the 6-paired endemics, except for one species, *C. kashmirica*, of northwestern India, are restricted to regions I to IV. In fact, two-thirds of them occur in the mountains of southwestern Europe and the Balkan Peninsula. But the 5-paired endemics are widely distributed, and the 4-paired species still more widely, with a strong representation in the Mediterranean littoral. The distribution of chromosome numbers among the endemic regions is consistent with the morphological evidence in showing that the oldest endemics are mostly in the mountains of southern Europe, whereas the youngest endemics are mostly in the Mediterranean littoral and closely adjacent areas. This evidence supports the general hypothesis, based on morphology and geographic distribution in the genus as a whole, concerning the origin and distribution of the genus. Chromosome number is considered here merely as one criterion of phylogenetic relations and not with reference to the genetic processes which made evolution possible (see next chapter, pp. 145-147).

It should be mentioned here, however, that the many changes in topography and the gradually increasing desiccation of the climate in southwestern Asia and the Mediterranean region must have been important causes of speciation. In *Crepis* the endemic areas most affected by these changing conditions are 1-9 and 21-24 (see fig. 10), where more than 60 per cent of the endemic species exist today.

The nature of the substratum is another environmental factor which may have had an important influence on the history of *Crepis*. The available data on the more primitive species are too scanty to permit an analysis; but the information at hand provides the following observations which may be significant. Although the most primitive endemic, *C. geracioides*, of the southern Balkan Peninsula, occurs on a serpentine formation, it is not known whether it is restricted to serpentine. Another Old World endemic reported to occur on serpentine is *C. gymnopus* of Hokkaido Island in the Japanese Archipelago. In North America the oldest species in their respective groups, *C. monticola* and *C. pleurocarpa*, have their "diploid" (22-chromosome) forms confined to the Mesozoic and Paleozoic rocks of the Klamath Mountains in northern California; and diploid *C. pleurocarpa* has been found only on serpentine and similar formations. Here is at least an indication that the restricted distribution of some of the primitive endemic species of *Crepis* is due, in part at least, to their peculiar edaphic requirements.

A similar relation between edaphic restriction and distributional restriction is found in such primitive endemics as *C. terglouensis*, *C. albiflora*, and *C. dioritica*. These species, like several other alpine relics, which occur locally but have somewhat wider distributions (*C. pygmaea*, *C. rhaetica*, *C. Jaquini*, *C. pontana*, *C. blattarioides*), are restricted to calcareous formations; whereas some of the most widely distributed primitive species (*C. paludosa*, *C. conzaefolia*) have been reported as occurring on both calcareous soils and soils deficient in lime.

THE BEARING OF ENDEMISM IN CREPIS ON PLANT DISTRIBUTION AND ON THE NATURE OF SPECIES

In addition to the support found in this study of endemism in *Crepis* for the phyletic history of the genus as a whole, it appears that some of the evidence on *Crepis* endemics has a significant bearing on certain problems of plant distribution and the nature of species.

Crepis and the age-and-area concept.—One distributional problem concerns the well-known age-and-area hypothesis (Willis, 1940) which assumes that the age of a species or group is proportional to the area it occupies (under certain specified conditions; cf. Gleason, 1924). From the foregoing review it is clear that among the endemic species of *Crepis* there are two extremely diverse groups: (1) *the primitive, perennial alpine endemics*, which are relatively old, monomorphic, and adapted to mesophytic conditions; and (2) *the advanced, annual, lowland endemics*, which are relatively young, more highly variable, and adapted to xerophytic conditions.

The present distribution of these two groups does not conform to the age-and-area hypothesis. The old, alpine endemics, however, are believed by most students of floristics to have been more widespread before the Pleistocene epoch and to have moved, from glacial refugia, into the narrow niches that they now occupy (Braun-Blanquet, 1923, pp. 260–261). The fact that many of them are of relatively wide distribution, although they exist only in a special type of environment, supports this idea. On the other hand, the young, lowland, annual endemics are just as widely distributed as the alpine species are at present; and there are a number of lowland, annual species, not endemics, *C. foetida* and *C. pulchra*, for example, which are about as widely distributed as the forerunners of the alpine endemics ever could have been. Hence, the age-and-area concept breaks down completely with respect to these two groups of endemic species. As has been pointed out by Stebbins (1941), the concepts of "senescence" and "competition" are no more satisfactory than age-and-area in attempting to account for such diverse groups of species. But the concept that the monomorphic, alpine species are genetically homogeneous and that the variable, lowland species are genetically heterogeneous, i.e., composed of several or many biotypes, provides an acceptable explanation of their differences in variability and distribution.

The nature of the "narrow" Crepis endemics.—This genetic approach to the problem of the differences between the widely distributed alpine and the lowland endemics also provides a satisfactory explanation of the nature of the "narrow" *Crepis* endemics. Of the forty-eight Old World species which were classified as "narrow," many are known only from their type locality or from vague information about their distribution. But there are several concerning which it is possible to make fairly definite statements. In their phylogenetic groups, these species, together with pertinent data, are as follows.

NARROW ENDEMICS—ALL PRESUMABLY MONOMORPHIC

Primitive

1) *C. kilimandscharica*. Section 8. Known only from Mt. Kilimanjaro at four stations, 2,700–3,500 meters, in forest.

2) *C. cameroonica*. Section 8. Known with certainty only from Mt. Cameroon at three stations, 2,000–4,000 meters, in meadows.

Intermediate

3) *C. taygetica*. Section 10. Known from five collections, all made at a place called "Porta," at about 2,300 meters altitude on Mt. St. Elias in the Taygetos Mts. of southern Greece. Exposed rocks.

4) *C. crocifolia*. Section 10. Known from three or four collections made at a place called Megala Zonaria, at about 2,400 meters altitude on the same mountain as the preceding. Exposed rocks.

5) *C. athena*. Section 10. Seven collections, all on Mt. Athos, Hagion Oros Peninsula, northern Greece. Exposed rocks.

Advanced

6) *C. eritreensis*. Section 20. Three or four collections at localities in southern Eritrea from 800 to 1,400 meters elevation. One collection was from "a comparatively moist, rocky formation."

7) *C. tybakiensis*. Section 20. Known from one specimen collected in southern Crete. Since Crete has been botanized by numerous collectors, it is very probable that this species would be represented by more collections if it were widely distributed on the island. Certainly insular.

8) *C. divaricata*. Section 25. The population on Madeira Island is restricted to the isolated eastern promontory, where it has been nearly exterminated by grazing. (This species, considered as a whole, is classified as polymorphic in table 1 because of the variant specimens collected in 1837–1850 from the tiny Desertas Islands near Madeira.) Certainly insular.

9) *C. Noronhaea*. Section 25. Six collections, all from Porto Santo, a small island in the Madeira Archipelago. Certainly insular.

10) *C. Forskalii*. Section 27. Two localities in Yemen province, southwestern Arabia, between 1,300 and 2,500 meters elevation, in the coffee belt.

It is noteworthy that three of these species, *C. divaricata*, *C. Noronhaea*, and *C. tybakiensis*, are insular and of very restricted distribution. They are, however, relatively advanced species. Therefore, their morphological homogeneity (assuming that *C. tybakiensis* is actually monomorphic) must be due to genetic homogeneity rather than to senescence. Five others in the above list, *C. kilimandscharica*, *C. cameroonica*, *C. taygetica*, *C. crocifolia*, and *C. athena*, are each found on only a single mountain. They are almost certainly "depleted" species (Stebbins, 1942a), and they probably became isolated through widespread changes in topography and climate during late Tertiary and Pleistocene times. In these, also, the population must be relatively small and homogeneous. The other two species, *C. eritreensis* and *C. Forskalii*, may also be "depleted" species, although it must be admitted that the available information on their distribution and variability is scanty. It is probable that all of these narrow endemics had their origin in Tertiary times or not later than Pleistocene (see p. 109). Therefore, since they are not of relatively recent origin, the genetic view that they are descendants of populations which were formerly more widespread, and that restriction of area has been accompanied by depletion of biotypes and genes, seems the most reasonable concept of their nature. It has been pointed out to me by M. K. Elias (*in litt.*) that the concept of "senescence" is hardly a realistic concept, since it is based on analogy, not on homology, with the life cycle of an individual. He also suggests that *Crepis* may be in a stage of "contraction" in the sense of Simpson (1940). Although this idea is hardly applicable to the genus as a whole, it may apply to certain sections or to certain types of species, such as the narrow endemics. Because the narrow *Crepis* endemics, both the insular and the continental species, are not "young" species in the sense of Willis, they do not conform to the age-and-area hypothesis any better than the two groups of widespread endemics discussed above.

SUMMARY

1) The twelve endemic regions for *Crepis*, comprising twenty-five areas, define the east-west distribution of the genus in the Old World almost completely.

2) Seventy-two per cent of the Old World *Crepis* species are endemic in the sense that they are restricted to a single subcontinental geographic area. Among these endemic species are two very diverse groups, namely, the most primitive, perennial species, half of which are alpine relics, and the advanced, annual species, most of which occur at low altitudes under arid conditions. The remaining endemics comprise an intermediate series connecting these two extremes. Only a comparatively few of the alpine perennials and the lowland annuals have narrow distributions, i.e., their distributional areas, as at present known, are mostly more than 150 kilometers in extent. From this evidence it is inferred that the alpine relics were formerly of wider distribution and that they moved into their present niches from glacial refugia; whereas the lowland, annual endemics have become adapted to a more arid climate, under conditions, however, favoring genetic heterogeneity. From the evidence on morphology and distribution, as well as on chromosome numbers, it is inferred that the process of adaptation from mesophytic to xerophytic conditions went on in the genus as a whole over a long period of time.

3) The distribution of the most primitive and the most advanced endemic species of *Crepis* supports the conclusion, derived from the evidence on phylogeny and distribution of the genus as a whole, that the center of origin was in Central Asia.

4) The age-and-area concept of Willis is completely at variance with the evidence on the two diverse groups of widespread endemic species mentioned above.

5) The concept of "senescence" fails to explain the existence of narrow endemics in *Crepis*, since this group includes some of the most primitive and most advanced species in the genus. Since they are either insular or "depleted" continental species, the population is more or less restricted in size and is relatively homogeneous. They also fail to conform to the age-and-area hypothesis.

CHAPTER 8

THE ORIGIN, MIGRATIONS, AND EVOLUTION OF CREPIS

THE PRESENT distribution of *Crepis* is of general interest in connection with the floristic history of the world, since it involves not only the Northern Hemisphere and the eastern continent (Eurasia), but also Africa and North America. Hitherto, the relation of this genus to vegetational history has not been recognized because (1) the genus has not been studied previously as a whole, and (2) the significance of the few fossil specimens of *Crepis* at present available (see pp. 132-134) has not been recognized. The dangers of basing phylogenetic assumptions only on the morphological relations and geographic distribution of existing species are well known. But when the systematic treatment of a unit-group rests on the synthesis of evidence from several different disciplines, and these various lines of evidence are all consistent with one another in their phylogenetic implications, as well as with the fossil evidence, which is true in *Crepis*, then surely one is warranted in erecting a hypothesis concerning the most probable region of origin of the group, its approximate age, and the probable migration routes over which it was distributed in order to explain its present distribution. All this, provided, of course, that the hypothesis can be shown to be consistent with the general principles of earth history and plant development as established by the known facts of geology and paleontology, especially paleobotany.

The earlier concept of the present author (Babcock, 1936), that the center of origin of *Crepis* and its closest allies was probably situated in southwestern Asia, was based on less complete evidence than is now available and without attempting to correlate the evidence on *Crepis* with the known aspects of vegetational history in the Northern Hemisphere, particularly in Eurasia. This correlation has now been established, with the result that the center of origin of *Crepis*, and of many closely related genera, appears to have been situated in the northern part of Central Asia, more specifically in the Altai-Tien Shan Mountains and adjacent steppes and plains. Having already reviewed the chief lines of evidence on which this conclusion is based, the present chapter will present an outline of the probable course of development of the genus. But first it is necessary to consider two pertinent questions: (1) Is *Crepis* really an ancient genus? (2) How well adapted is *Crepis* to plant migration?

THE ANTIQUITY OF CREPIS

From the preceding review of the geographic distribution of the Crepidinae, it is obvious that this subtribe must have originated before the Pleistocene age. The world-wide distribution of *Hieracium* is enough in itself to establish this fact. During Pleistocene, especially in the time of maximum glaciation, the holarctic spread of many species and the extension of the subgenus *Stenotheca* into North and South America could not have occurred. It is probable, as shown by Engler (1879), that the holarctic distribution of *Hieracium* occurred in post-Pleistocene times. But that the spread of the subgenus *Stenotheca* from Asia via North America to the southern tip of South America and the development of the derived subgenus *Mandonia* in the Andes could have been accomplished in such a relatively short time is unthinkable, even in plants with wind-borne seeds. Hence, in formulating a hypothesis, we are forced to go back at least to the Tertiary period. The present distribution of several other large genera of the Crepidinae, such as *Prenanthes* and *Lactuca*, indicate a corresponding antiquity.

In *Crepis* the distributional evidence agrees completely with the foregoing. Sharsmith (1940) concluded that *C. nana typica* reached the Sierra Nevada of California between the Pliocene and the Wisconsin stage of the Pleistocene (see p. 140). On this basis it is safe to assume that its origin in Asia occurred as early as the Pliocene or earlier. It was shown by Babcock and Stebbins (1938, pp. 34-36) that the period during which the eight diploid, 11-paired North American species could have originated and migrated into the region they now occupy is limited to Miocene, Pliocene, and early Pleistocene; also, that the four older species probably originated about the middle of this period, i.e., in late Miocene, whereas the four younger species were most probably formed during the latter part of the period, i.e., in mid-Pliocene or early Pleistocene time. Since it is practically certain that all these species originated through hybridization between diploid Asiatic species with lower chromosome numbers, it is fairly certain that the most primitive species of *Crepis* had their origin at least as early as Middle Miocene. But the gap which exists between these most primitive *Crepis* species and their putative ancestors in *Dubyaea*, both in their morphology and in their chromosome numbers and karyotypes, must indicate a developmental period of considerable length. Hence, the period during which *Dubyaea* flourished and during which the main phylogenetic lines of the Crepidinae had their origin and early development, may safely be considered to be as early as the beginning of the Miocene epoch. They may have existed even in Oligocene or late Cretaceous. The possible correlation of the history of the Crepidinae with that of the Artiodactyls (see p. 133) suggests such an early origin for the ancestors of *Crepis*. Since, however, the Miocene epoch has been estimated by various authors to have lasted from twenty to thirty million years, it would seem hardly necessary to go further back than late Oligocene for the origin of *Crepis*.

Fortunately, there is some fossil evidence which establishes beyond much doubt the existence of *Crepis* in the Tertiary period. Reid and Reid (1908, 1916) reported seeds of three species of *Crepis* from the Middle Pliocene Reuverian beds at Swalmen and Reuver in southeastern Holland, near the border of Germany; also, of one species from the Upper Pliocene Cromerian beds at Pakefield, Suffolk, England. Three of these four fossil species have been definitely identified. These are illustrated in plate 1, along with present-day achenes of the same species. (The fourth species was identified by Reid and Reid [1916] as *Crepis fuscipappa* [now *Youngia fuscipappa*] and, along with the one fossil seed [in their pl. 17, nos. 28, 29], was shown, as supposedly corroborative evidence, a present-day achene of *Youngia cineripappa* Bab. et Stebbins from China. But *Youngia fuscipappa* occurs only in Ceylon. This fossil seed is very probably not a species of *Youngia*, since that genus is restricted to eastern Asia. Judging only from the lithograph, this fossil is not well enough preserved to make identification possible, although it may be a species of *Crepis*.)

In plate 1, *a* and *a'* show one fossil and two present-day achenes of *Crepis terglouensis*. This fossil was originally reported as *Crepis* sp. by Reid and Reid (1916, pl. 17, no. 30), who must have had no present-day achenes of this species with which to compare the fossil, because the resemblance is perfect in every observable detail. Even the cracked and flattened base of the fossil achene, which at first glance appears broad and notched, would correspond with the rather narrow base in the perfect achenes, if it could be restored. In plate 1, *b* and *b'* show two fossils and two present-day achenes of *Crepis conyzaefolia*. The two fossils were identified as *C. blattarioides* (Reid and Reid, 1916, pl. 17, nos. 26, 27). Although they fall within the size range of that species, the ribs are too few and much too wide for *C. blattarioides*, whereas they very closely resemble those of *C. conyzaefolia*; also, the over-all size is within the range of this species.

These fossils of *C. terglouensis* and *C. conyzaefolia* were found in the Reuverian beds in southeastern Holland, which formation was identified by Reid and Reid (*op. cit.*) as most probably Middle Pliocene. That district, according to the authors, was included in the extensive delta of the Rhine and Maas rivers during certain parts of the Pliocene epoch. These great rivers evidently brought down from the northern slopes of the Alps vast quantities of plant material which were deposited in the estuary. Along with seeds and fruits of hundreds of other species, these *Crepis* fruits were recovered from the clay pits of Limburg and near-by Germany.

The third *Crepis* species which is represented by a reported fossil is *C. mollis* (*C. succisaefolia* of Reid and Reid [1908, p. 217, pl. 13, no. 96]). Fossil seeds of this species were reported as not uncommon at Pakefield, where they were found in clay deposits determined to be Upper Pliocene. *C. mollis* is a widespread species of central and northern Europe and occurs at the present time in England. The fossil achene is reproduced in plate 36, c, and, with it, c', are two present-day achenes. The resemblance is very close. The fossil specimen falls within the known range of length, but it is a little broader than the broadest achene of this species available to me, and the ribs, though the same in number, are somewhat wider. It might well be assumed that the differences mentioned are due to the reduction in width of fruits and ribs which has accumulated in this species during the Quaternary period.

It should be mentioned that fossil achenes of *Crepis capillaris* have also been reported (as *C. virens*) by Reid (1898, 1899) as occurring in late Glacial and Neolithic deposits in Scotland.

The fossil fruits of *C. terglouensis*, one of the most primitive 6-paired species, and of *C. conyzaefolia*, the most primitive 4-paired species, are especially significant in establishing the age of *Crepis*. The fact that these species existed on the northern slopes of the Alps in pre-Pleistocene times, and probably as early as Middle Pliocene, calls for a considerable interval of time during which they could have migrated from Central Asia, a straight line distance of more than 6,000 kilometers. In view of this evidence it is necessary to assume that *Crepis* originated at least as early as the Miocene epoch.

This assumption is in good agreement with the general scheme of phyletic change in the Compositae by Small (1919, p. 297), in which he shows the Lactucinae (= Crepidinae) as differentiating into subtribes in Miocene. Furthermore, Small (*op. cit.*, pp. 321–326) emphasizes the importance of the Miocene epoch for the differentiation of the Compositae throughout the world, by stating that at or before Middle Pliocene most of the subtribes of the Compositae had been differentiated and that Upper Pliocene and later times were characterized by generic, specific, and varietal differentiation rather than by the origin of larger groups.

Significant, if true, is the paleogeographic evidence found in the Miocene continental outlines (cf. fig. 6, lower map). The broad peninsula extending from Central Asia westward into Tethys as far as the European Alps, and the continuous land across Arabia to Africa, provided land routes for the most primitive species of *Crepis* into southern Europe and tropical Africa during Miocene.

An established fact of possible significance for the antiquity of *Crepis* is the present occurrence of certain primitive, endemic species (*C. geracioides* of Albania, *C. gymnopus* of Japan, and the 22-chromosome form of *C. pleurocarpa* of northern California) on serpentine formations. Furthermore, those formations on which *C. pleurocarpa* is found are associated with other Mesozoic and Paleozoic rocks.

In this connection it may also be significant that in a recent and thorough evaluation of the evidence bearing on the origin and distribution of the Artiodactyl

ungulate mammals Pilgrim (1941, pp. 153–156; 161–162) concludes that the sub-order Pecora, which includes such ruminants as deer, antelopes, goats, sheep, oxen, and giraffes, had its origin in Central Asia, from whence it spread over the world. The pecoran families, according to Pilgrim, branched off from the more primitive Tragulina probably in the Oligocene epoch. If this is true, they must have been developing and migrating throughout the Miocene. Pilgrim (*op. cit.*, p. 155) refers to Miocene fossils from Europe, Mongolia, and North America which support this inference. Many species of *Crepis* are associated today with grasses and other herbs of importance as forage for ruminants; and some *Crepis* species are so acceptable to sheep and cattle that botanical specimens are sometimes extremely difficult to find on areas that have been grazed recently. It is not unlikely, therefore, that the development and migrations of the Crepidinae were contemporaneous with, or antedated, the development and migrations of the Pecora from Central Asia throughout the world.

In view of all the evidence, the conclusion is warranted that *Crepis* had its origin, early dispersal, and beginnings of differentiation about the middle of the Tertiary period, either in early Miocene or late Oligocene.

THE ADAPTABILITY OF CREPIS TO MIGRATION

As was pointed out by Engler (1916), plant migration is generally dependent on the germinability, viability, and transportability of the seeds, as well as the existence of favorable environmental conditions in the region invaded. Most *Crepis* species reproduce exclusively by seeds, and in those few which are mat-forming or which reproduce by stolons, viable seeds are also produced. Although some of the high montane, primitive species have proved rather difficult to propagate from seeds under artificial conditions, yet where it has been possible to imitate natural conditions rather closely the seeds have usually germinated satisfactorily. Only in *Crepis pygmaea* has it not yet been possible to obtain plants from seeds collected the previous year in the Alps, although several attempts were made; as a result, our cultivated specimens had to be grown from roots collected in the wild. It happened, however, in *C. pygmaea* that the best method of germinating the seeds of alpine species—subjecting the seeds to more nearly natural conditions by placing them outdoors in a flat at a montane elevation where they would be covered by snow in the winter, with consequent spring thawing and freezing—was not used. It is probable that seeds of *C. pygmaea* would have germinated under such conditions.

Great variation exists with respect to the length of viability of the seeds of *Crepis* species. It is safe to assume, however, that the seeds of all species remain viable for at least one year, since it has been possible to propagate many of the species from seeds more than one year old. In this connection the difference between *C. capillaris* and *C. tectorum* in seed viability is of considerable interest. Navashin, Gerassimova, and Belajeva (1940) reported a striking difference between the two species in the effect of storage on germinability of the seeds and viability of the seedlings. At the end of two and a half years all the seeds of *C. tectorum* had nearly lost the ability to germinate, and the viability of the few seedlings obtained was almost nil, whereas the seeds of *C. capillaris*, as had been observed in early experiments, showed much greater resistance. The distinction between the two species, it was pointed out, is an important adaptation. *C. capillaris* is a typical annual, and its achenes normally germinate in the spring after a period of eight or nine months of dormancy, whereas *C. tectorum* is a "winter plant," i.e., its seeds germinate soon after maturation, the vegetative rosettes live through the winter even in Russia, and the plants

flower the following spring or early summer. It will be noted, however, that even in *C. tectorum* the seeds retain their viability for two years in sufficient degree to maintain the species. Perhaps the most striking correlation between high specialization and length of seed viability is found in *C. senecioides*, a precocious desert annual the tiny seeds of which remain viable for at least twelve years and possibly longer.

As for transportability, the seeds of most species of *Crepis*, with their abundant pappus, are especially adapted for transport by wind. In the most primitive species the seeds are light and the pappus is relatively large. Even in *C. kashmirica* the very coarse ribs of the achenes are merely folds enclosing white, spongy tissue; and a single dry seed, containing an embryo, weighs only about two milligrams. In a gentle breeze, such a seed, even with its pappus intact, tends to fall rapidly toward the earth; but in a strong wind it is possible for it to be carried great distances. Hegi (1929) reports the observation of an immigrant colony of *C. alpestris* in a newly excavated gravel pit to which the achenes must have been carried at least three kilometers distance from the nearest mother plants. *Crepis* is classified by Ridley (1930) as being dispersed by wind, by adhesion to animals, and by human agency. He also states that the seeds can be dispersed by water, since he observed seeds of *C. biennis* remaining afloat for one and a half days. In *C. patula*, which has extremely short pappus, the seeds remain enclosed in the strongly indurate involucre. This species often grows on stream banks, and it is probable that old, broken-off involucres full of seeds are sometimes transported by the streams. The same might be true of its close relative, *C. Zacintha*. Ridley reports no evidence on dispersal of *Crepis* by birds, but *Taraxacum* is mentioned in one such list. It is possible that some of the wider gaps in distribution among the primitive species found on the high mountains of tropical Africa would best be explained through dispersal by birds. But, in addition to all other natural methods of seed distribution in *Crepis*, dispersal by wind is undoubtedly efficient enough to account for very extensive migration and for wide gaps in distribution.

Concerning wind dispersal in the Compositae as a whole, Small (1919) concludes that the evidence from Krakatau is confirmed by the observations on Taal Island (in Bombon Lake, Luzon) and that there remains no doubt whatever about the usual dispersal by wind of a number of Compositae to distances of 4 to 20 miles and the occasional dispersal of pappose fruits to distances of more than 100 miles. Small (*op. cit.*, 169–177) conducted a critical experiment on the aerodynamics of fruit dispersal in *Taraxacum officinale* from which he concluded that the conditions necessary for long distance dispersal of seeds are: (1) low relative humidity of the atmosphere; (2) a wind constant in direction and always above a certain minimum velocity (for dandelion seeds, about 2 miles per hour). He concludes that, given these conditions, there is no limit to the dispersal of pappose fruits. He states further that such conditions occur occasionally in most of the regions in which long-distance dispersal has been observed. There would seem to be little if any doubt that such conditions must have existed occasionally during periods when *Crepis* fruits would have been ready for dispersal throughout southwestern Asia and northern Africa. It is possible, therefore, that *Crepis* species were distributed by wind from one mountain to another across tropical Africa, or from one range to another across northern Africa, and even from the African mainland to the Madeira and Canary Islands, distances of 100 and 700 kilometers, respectively (about 60 and 400 miles). The conclusion of Cockerell (1928) that seeds were carried from the mainland to the Madeira Islands by birds appears to be warranted, since the distance from the mainland is small and no less than seventy species of birds have

been reported as visitors or stragglers to Madeira. But the evidence of Danish investigators (cf. Warming, 1903, p. 676) is definitely against such a conclusion being applied to the Canary Islands.

The relative importance of the wind and all other possible agencies in establishing the present flora of the Faeröes, the group of small islands lying 400 kilometers (nearly 250 miles) north of Scotland, received careful consideration by Warming (*op. cit.*), whose studies on the floras of isolated north Atlantic islands are outstanding. He reaches the general conclusion that the whole of the flora—at least all the more highly organized land plants—have migrated to the Faeröes since the glacial period, across the sea, and from the nearest countries, especially Great Britain. Man, he points out, has undoubtedly been responsible for the introduction of the weeds and some of the other lowland species. But at least 60 per cent of the vascular species must have depended upon other agencies for transportation. Although a few species may have been brought by ocean currents, and some others, especially those with heavier seeds, possibly by birds, yet it seems probable that the wind was the most important agency in transporting the seeds of most of these plants. Regarding the general importance of winds as an agency in plant distribution, Warming (*op. cit.*, p. 679) reaches the conclusion that “On the whole I am unable to find an explanation for the different phenomena respecting the distribution of plants, unless I adopt the theory that germs of all kinds are being sown constantly and in every direction, and that it is chiefly by the agency of the wind that the sowing and colonization of the earth is effected across longer distances.”

ECOLOGICAL RELATIONS OF CREPIS

The ecological relations of *Crepis* are extremely varied. But, for purposes of the present discussion, the species can be roughly classified by sections according to temperature and moisture relations as follows:

- A. Temperate, mesophytic—sections 1, 5, 7, 8.
- B. Temperate-alpine, mesophytic—sections 3, 6.
- C. Alpine or arctic-alpine, mesophytic—sections 2, 4, 12.
- D. Temperate, mesoxerophytic—sections 9–11, 13–21, 23–25.
- E. Temperate, xerophytic—sections 22, 26, 27.

Almost all of the species are adapted to a temperate climate, and the most primitive ones (secs. 1–8) are definitely mesophytic. Among these primitive species there are several, most notably those of sections 3 and 6, with wide altitudinal ranges, i.e., they occur in locations ranging all the way from temperate (or even warm-temperate) up to alpine climates. The same is true to a more limited extent for *C. sibirica* and *C. paludosa* of section 1. These wide altitudinal ranges certainly indicate a marked adaptability in these species which is directly correlated with such wide geographic distributions as those of *C. sibirica*, *C. paludosa*, and *C. conyzae-folia*. When these species are found in subalpine or alpine locations, it may be assumed (cf. p. 103) that in some earlier epoch climatic conditions favored their migration upward, from a more extensive distribution at lower altitudes, and that subsequent environmental changes resulted in the establishment of local alpine populations (cf. *C. pygmaea*, Part II, p. 242). In such a species as *C. rhactica* and the strictly alpine species of sections 2 and 4, the same sort of earlier history can be assumed, except that subsequent climatic changes completely exterminated the forms of these species which existed earlier at lower levels. This Englerian hypothesis, which has been accepted by Braun-Blanquet (cf. p. 104) and many others, is accepted here as the best explanation of the present distribution of the alpine endemics in *Crepis*. In the more advanced sections there is an increasing number

of xerophytic species which is directly correlated with the fact that these species were differentiated in south Central and southwestern Asia and the Mediterranean region during Pliocene-Pleistocene at times when these regions became extremely arid. This sweeping statement applies only in a general sense. In all of the more advanced groups (secs. 9–27) we find more or less variation between the species of a section with respect to water relations, indicating that they evolved under various local conditions.

ORIGIN, MIGRATIONS, AND DEVELOPMENT OF CREPIS

Origin.—Like the other primitive generic types in the Cichorieae, the earliest *Crepis* species probably developed from *Dubyaea*-like species which had already evolved from less specialized ancestors living in northeastern Asia (Angara). That the progenitors of *Dubyaea* could have originated somewhere east of Lake Baikal and moved westward into the Altai region is not an unreasonable hypothesis. Although there is available to me no present-day or fossil evidence to support the idea, yet it is in line with the observation of Kryshstofovich (1933, p. 121) that in the Ussuri region, north of Vladivostok, there is clear evidence that in Lower Cretaceous time there began a new development of plant life. He suggests that this came about through the immigration of new elements which had developed in or near the glaciated region (to the north, see p. 93) and which united with the Paleozoic flora of Angara to give a new start to the plant world.

The closest living relatives of these assumed ancestors of *Crepis* are the most primitive species of *Dubyaea* (cf. Stebbins, 1940, p. 52), namely, *D. oligocephala*, *D. hispida*, *D. atropurpurea*, and *D. chimiliensis*, the first two of which are known to have 8 pairs of chromosomes (Babcock, Stebbins, and Jenkins, 1937). It is assumed that in the *Dubyaea*-like ancestors of *Crepis* the chromosome number had already been reduced from 8 to 7, since the most primitive *Crepis* species have 6 and 5 pairs of chromosomes.

It is probable that these earliest *Crepis* species developed in the Altai-Tien Shan region of Central Asia. This hypothesis is based on the present geographic distribution of *Crepis* and related genera. This American-Asiatic-European-African distribution resembles that of many other genera, some of which, like *Cedrus* and *Datisca* (pp. 98–100), appear from the fossil evidence probably to have originated in Asia. Strong precedents are found for accepting this hypothesis in the conclusions reached by Engler (p. 102) regarding *Aconitum*, *Pedicularis*, *Saussurea*, and many other genera; by Schwarz (p. 106) for *Laurentia tenella*, *Pinus Peuce*, and other species; by Czeaczott (1937) for *Datisca cannibina* and other Colchic-south Euxine plants; and by Hagen (p. 107) for a great many xerophytic species that migrated from Asia into north Africa. For reasons already stated (pp. 131–134) it is probable that these earliest *Crepis* species appeared about the middle of the Tertiary period.

Early development.—1) The rhizomatous species.—The most primitive species, *Crepis sibirica*, *C. geracioides*, *C. viscidula*, and *C. paludosa* (sec. 1), have a rhizome instead of a true root; and since they now occur in a temperate climate and in moist locations, it is assumed that their *Dubyaea*-like ancestors inhabited moist places in the lower montane regions. The other primitive rhizomatous species (sections 2, 3, 4, and 5) probably had a relatively early origin, since, even though their development occurred under a variety of conditions, they all contain 6-paired species. The species of sections 2, 3, and 4 became adapted to much higher elevations in the mountains and to various types of soils; whereas the more primitive species of section 5, *C. lapsanoides*, *C. lyrata*, and *C. mollis*, occupied habitats more like

those of section 1. Similarly with section 13, *C. gymnopus* became differentiated in connection with adaptation to alpine conditions, whereas *C. praemorsa* is a low-land species. Three of the species in section 21 are alpine or high montane and the other one, *C. Gmelini*, occurs in eastern Siberia at about the 60th meridian. All four of these species have become adapted to much colder climates than those suitable for sections 1 and 5.

2) The primitive taprooted species.—The taprooted species probably developed from rhizomatous ancestors. Evidence for this has been presented (pp. 43, 70) in connection with *C. rhaetica*, *C. Reuteriana*, and *C. Bungei*. Furthermore, a marked resemblance was noted between *C. pontana*, the most primitive taprooted species, and the species of sections 1 and 2. It seems very probable that the early types with a deeply penetrating taproot became established in connection with adaptation to drier situations. At any rate, the other species of section 6, like *C. pontana*, came to occupy high montane habitats. Furthermore, the section 2–section 6 line seems to have developed in the southern part of the region of origin, whereas the foundation stock of section 4 began rather early to spread both to the northeast and southwest. In the more southern part of the general region of origin, also, the progenitors of sections 7, 8, 9, 10, and 11 must have begun their development during this earlier period in the history of the genus.

3) The probable status of the genus in early Miocene.—From the foregoing considerations (chaps. 4–7) and evidence given under individual species (Part II), it may be assumed that in the early part of the Miocene epoch the more primitive rhizomatous species were already differentiated into geographical and ecological groups. *C. sibirica*, *C. paludosa*, and *C. mollis* were probably abundant at lower elevations between the Altai and the Ural Mountains; whereas *C. geracioides*, *C. viscidula*, *C. pygmaea*, *C. lapsanoides*, and some other members of section 6 were probably distributed in the southwestern part of north Central Asia at various elevations. *C. hokkaidoensis*, *C. chrysantha*, and *C. gymnopus* were already distributed at high elevations toward the northwest. Certain species, *C. terglouensis*, *C. Jacquini*, and *C. rhaetica*, which are now relics in the European Alps, were probably distributed at high elevations in the southwestern part of the region of origin; whereas *C. pontana*, *C. conyzaefolia*, *C. blattarioides*, *C. aurea*, *C. albida*, and *C. tingitana*, as well as *C. kilimandscharica*, *C. alpestris*, and their closest relatives in section 8, occurred at somewhat lower elevations in the same region.

By late Miocene the more primitive species of several other sections were probably established mostly in the Tien Shan–Betpak-dala uplands, such as *C. Strausii*, *C. darvasica*, *C. songorica*, *C. sonchifolia*, *C. auriculacfolia*, and *C. Raulini* of section 10; *C. Schachtii*, *C. Hookeriana*, *C. bithynica*, *C. armena*, and *C. tencerrima* of section 11; *C. connexa* of section 16; *C. Reuteriana* of section 19; *C. alpina* of section 20 or a less-specialized form of it; and *C. patula* of section 23. But *C. orcadensis* of section 11 and *C. Bungei* of section 14 were distributed more to the east.

Sections 12, *Ixeridopsis*; 15, *Psilochaenia*; and 18, *Pyrnachos*, require separate treatment. The *Ixeridopsis* group, one member of which, *C. nana*, is now distributed from south Central Asia to northeastern North America, probably originated in the Tien Shan region as early as the most primitive species of *Crepis*. It seems probable that the whole group originated through hybridization between one or more *Crepis*-like *Dubyaea* species and one or more *Ixeris*-like *Dubyaea* species, all of which had 7 pairs of chromosomes. The indigenous North American species, section *Psilochaenia*, are believed to have originated through several different hybridizations involving species in sections 2, 4, 11, 12, 13, and 14, or similar now-extinct species. It is probable that all of these putative ancestors of the American

group were distributed in the eastern part of the region of origin or had already migrated farther to the northeast before hybridization occurred. *Pyrinachos*, section 18, may have arisen independently from the ancestral stock from which *Ixeris*, *Youngia*, and *Crepis* arose, or from hybrids between these lines before they were sharply differentiated. In either event, their origin probably occurred in the southern part of the region of origin of *Crepis*. The probability that this is true is considerably increased by the fact that both *Ixeris* and *Youngia* have their present distribution for the most part in E. and S.E. Asia.

Migration and later development.—1) East-west migration from north Central Asia.—After the region southeast of the Ural Mountains had emerged from beneath the Obic Sea and the higher Kirghiz steppes were thus extended westward into "Russia," *C. sibirica*, *C. paludosa*, and *C. mollis* could spread over northern Europe. The last two species were much more aggressive than *C. sibirica*, which may never have reached the Atlantic coast. With increasing cold during Pliocene, these species all moved southward, *C. paludosa* and *C. mollis* eventually finding Pleistocene refugia in southern Scandinavia, the British Isles, and the southern mainland; whereas *C. sibirica* was limited to a few localities in the Sudeten-Carpathian region. It was probably during the cooler Pliocene epoch that the alpine *C. multicaulis* migrated across the Urals and arctic Russia to northern Scandinavia where it persisted as a nunatak species during Pleistocene. About the same time, *C. praemorsa* moved both eastward across Siberia and westward into Russia, across the Ural-Caspian land area, and gradually extended its area to the west until it reached the southeastern Alps, where *C. incarnata* originated. Meanwhile, *C. panonica* had originated, presumably in Betpak-dala, and followed a migrational course similar to the western trend of *C. praemorsa*, but somewhat more southerly. When it reached the northwestern Balkan Peninsula and Italy, probably in Pleistocene, it gave rise to *C. latialis*, *C. chondrilloides*, and possibly *C. bertisceae*. It may be that the progenitors of the two octoploid species, *C. ciliata* and *C. biennis*, also reached the Caucasus over a route north of the Caspian Sea. At any rate, the origin of these two polyploids probably occurred in the Caucasus Mountains during Pleistocene. Their ancestors are believed to have been related rather closely to the ancestor of *C. nicaeensis* (Part II, pp. 439, 769), and they may have been related to the ancestor of *C. oporinoides* of S. Spain (Part II, p. 474).

2) Northeasterly migration from Central Asia.—*Crepis sibirica*, in addition to its migration into Europe, also extended its range to the northeast and east of the Altai region. Also, *C. hokkaidoensis*, *C. gymnopus*, and *C. chrysantha* continued their northeasterly movement, the first two probably reaching their present localities during Pliocene or Pleistocene when what is now the Japanese Archipelago was still a peninsula extending south from Amur. These species, of course, found plenty of refugia along their route during maximum glaciation. The spread of *C. chrysantha* over the arctic tundra into the Urals and northeastern Europe undoubtedly took place in post-Pleistocene time. Probably it was during this later epoch also that the tetraploid *C. polytricha* arose; also, that *C. Bungei* and *C. tectorum* of section 14 had their origin in Siberia from *C. ircutensis* or similar ancestors. The distribution of *C. oreades* of section 11 in its eastern extension probably overlapped that of *C. Bungei*; but *C. oreades*, being distributed much farther to the southwest than *C. Bungei*, eventually reached the Pamirs. In this respect *C. oreades* shows a tendency to follow the general migration trend of all the species in its section except *C. crocea*. The former is probably an amphidiploid derived from a hybrid between *C. crocea* and *C. Bungei*, and, like other aggressive polyploids, it was able to extend its range far beyond those of the parents, reaching Manchuria to the

northeast and Tibet to the south. The species which migrated into North America, *C. nana* of section 12 and the amphidiploid progenitors of section 15, undoubtedly moved across the Beringian land bridge at several different times. *C. nana*, because of its present stations in northeastern North America, was probably the first to cross from Siberia to Alaska and beyond. If the section *Ixeridopsis* did arise from hybrids between partly differentiated *Dubyaea* lines, their origin occurred earlier than mid-Miocene. The probable sequence of migrations of the older and younger foundation species of section *Psilochaenia* is reviewed by Babcock and Stebbins (1938, pp. 30-38).

3) The southeasterly migrations from Central Asia.—Of the *Crepis* species thus far discovered, only nine migrated in a southeasterly direction from Central Asia. These are *C. subscaposa* of section 8, the monotypic section, *C. napifera*, five species of *Pyrimachos* (sec. 18), and two species of section 21. Reasons have been given (p. 71) for assuming that *Pyrimachos* had a hybrid origin somewhat similar to that of section *Ixeridopsis*. It is therefore reasonable to assume that this group also originated rather early in the history of the Cichorieae, when *Crepis*, *Ixeris*, and *Youngia* were not sharply differentiated. And the region of origin of this section was probably in Central Asia, like that of *Youngia*. Being adapted to a warmer climate than most *Crepis* species, these species migrated to the southeast during Pliocene and found their way still farther southward during Pleistocene. The origin and migration of *C. napifera*, which now occurs in southwestern China and southeastern Tibet, is in general similar to that of *Pyrimachos*. It appears to have been an offshoot from a primitive *Dubyaea* line that resembled both *Crepis* and *Youngia*. In *C. subscaposa* a somewhat different situation holds. Although it has none of the distinguishing features of section *Pyrimachos*, it now occurs in the same general region as that group. Moreover, it belongs morphologically in section 8, which section, except for one species, *C. alpestris* of Asia Minor and southern Europe, is found entirely in Africa. It is necessary to assume, therefore, that *C. subscaposa* originated from the same ancestral stock that produced *C. kilimandscharica* and *C. urundica*, but that for some reason *C. subscaposa* migrated from southern Central Asia in a southeasterly direction instead of a southwesterly direction. Perhaps the parting of the ways took place in early Pliocene northeast of the Pamirs, and *C. subscaposa* found its way across Chinese Turkestan and Tibet during Pluvial times, whereas *C. alpestris* and the other primitive species of section 8 moved southwest across Russian Turkestan and Iran. It is not impossible that other species resembling those of section 8 may yet be discovered in southeastern Asia. That section 21 (*Microcephalum*) had its origin in Central Asia is practically certain, since *C. tibetica* and *C. elongata* occur in southeastern Asia, *C. Gmelini* in northeastern Asia, and *C. multicaulis* is distributed from the Himalaya to the Altai and in northern Norway.

4) The southwesterly migrations from Central Asia.—These migrations were by far the most important movements of *Crepis* species away from the region of origin, since they had the most profound effect on the present distribution of the genus. The general aspects of these migration trends, and their consequences for many groups of flowering plants, may be summarized as follows: (1) They continued over a very long time, including probably both the Mesozoic and Cenozoic eras. (2) Throughout this period migrations went on in two directions, i.e., from Asia westward and vice versa. (3) From mid-Tertiary onward the trend from Central Asia southwestward into the Mediterranean region and Africa became more and more pronounced. (4) During Pliocene and Pleistocene times the many topographic and climatic changes in southern Central Asia and the Mediterranean region re-

sulted in (a) the extinction in the eastern Mediterranean region of many of the more primitive types which had already become established in the Alps, the Iberian Peninsula, and the Atlas Mountains; (b) greatly increased speciation in those groups which still had representatives in the Turano-Iranian and eastern Mediterranean regions.

This increase in the number of species can be explained in terms of modern genetic theory. It is reasonable to assume, especially in plants well adapted for seed dispersal, that small subspecific populations would frequently become isolated in space at a given time. Also, isolation in time at a given place may have occurred as a result of sudden environmental changes. It has been shown by Wright (1931) that the effect of gene mutation, natural selection, and random fixation in a small population is the rapid reduction of genetic variability. It is highly probable that the genotypes fixed in different small populations of the same species would differ as a result of differences in mutations and environment. If the isolation of small subspecific populations were followed by the reestablishment of contacts between them through gradual expansion and overlapping of their continuous areas or through wind dispersal over intervening spaces, this would be followed by hybridization and the further operation of natural selection. Furthermore, the whole process might be repeated at a later period. Apparently the great increase in the number of species of *Crepis* in sections 8, 10, and 24–27 resulted from some such processes as the foregoing. The statement of Schwarz (1938), that the Armenian mountains served as a “gene filter” to reduce the number of biotypes in certain species, indicates his appreciation of the important role played by secular changes in the eastern Mediterranean region during Pliocene-Pleistocene in the evolution of the more advanced and specialized species of many plants, including *Crepis*.

The species of *Crepis* which migrated in a southwesterly direction from Central Asia may be divided into three groups. The first group consists of the more primitive species or more “aggressive” less primitive species that probably migrated during late Miocene or early Pliocene, reaching southern Europe and northeastern tropical Africa before the disruptive topographic and climatic changes in the eastern Mediterranean region could annihilate them. These species are listed below, each being preceded by its section number. The geographic distribution of each species is roughly indicated by the countries or regions in which it occurs. Names capitalized are the most primitive species in this group; names in lower case type are somewhat less primitive species.

GROUP 1

1. GERACIOIDES—N. Greece, Albania, Macedonia.
1. VISCIDULA—Albania, Serbia, Bulgaria, Rumania.
3. PYGMAEA—Tirol, Italy, Switzerland, France, Spain.
4. TERGLOUENSIS—Tirol, Austria, E. Switzerland.
4. RHAETICA—Switzerland, Tirol.
4. JACQUINI—Carpathians to Bavaria, Tirol, E. Switzerland.
4. aurea—N.W. Asia Minor, W. Balkan Peninsula to E. France.
5. LAPSANOIDES—Pyrenees, N. Spain, N. Portugal.
5. SMYRNAEA—N.W. Asia Minor, S. Greece.
5. montana—Greece.
5. Mungierii—Crete.
6. PONTANA—Bulgaria, W. Balkan Peninsula to Switzerland.
6. CONYZAEFOLIA—Altai, N. Iran, Asia Minor, Balkan Peninsula to Pyrenees.
6. BLATTARIOIDES—N.W. Balkan Peninsula, Tirol, Alps, Pyrenees.
7. ALBIDA—N.W. Italy, S. France, Spain, Balearics, N. Morocco.
7. achyrophoroides—N. Abyssinia.

8. KILIMANDSCHARICA—Mt. Kilimanjaro (Tanganyika).
 8. KENTIENSIS—Mt. Kenya (Tanganyika).
 8. ALPESTRIS—N.W. Asia Minor, W. Carpathians, W. Balkan Peninsula, W. Austria, E. Switzerland.
 8. SUFFRUTICOSA—Mt. Meru (Tanganyika).
 8. IRINGENSIS—Mporotos Mts. (Tanganyika).
 8. MERUENSIS—Mt. Meru, Mt. Kilimanjaro (Tanganyika).
 8. CAMEROONICA—Mt. Cameroon (W. tropical Africa).
 8. URUNDICA—Urundi (Belgian Congo).
 9. TINGITANA—N.W. Morocco, S.W. Spain.
 9. leontodontoides—N. Italy, S. France.
 10. AURICULAEFOLIA—Crete.
 10. BALDACCII—Balkan Peninsula.
 10. RAULINI—Crete.
 10. ALBANICA—Balkan Peninsula.
 10. GUIOLIANA—Balkan Peninsula.
 10. turcica—Balkan Peninsula.
 10. Pantocsekii—Balkan Peninsula.
 10. Triasii—Balearic Islands.
 10. macropus—W. Asia Minor.
 10. oporinoides—S. Spain.
 10. Sibthorpiana—Crete.
 10. incana—Greece.
 10. taygetica—Greece.
 10. crocifolia—Greece.
 10. athoa—Greece.
 11. SCHACHTII—S. Bulgaria.
 11. BITHYNICA—Asia Minor, Bulgaria.
 11. tenerrima—Abyssinia.
 11. xylorrhiza—Abyssinia.
 11. abyssinica—Abyssinia.
 11. Hookeriana—Morocco.
 11. Faureliana—S. Algeria.
 11. Robertioides—Syria.
 19. Reuteriana—S.W. Asia Minor, Cyprus, Syria, N. Palestine.
 23. patula—N. Tunisia, E. Algeria.
 24. nicaeensis—W. Balkan Peninsula, N. Italy, S.E. France, S. Pyrenees.
 25. spathulata—Sicily.
 25. Salzmannii—N. Algeria, N. Morocco.
 25. Clausonis—N. Egypt, N. Tunisia, E. Algeria.
 25. Fontiana—N.W. Morocco.
 25. Bourgeaui—N. Morocco, S. Spain.
 25. canariensis—Canary Islands.
 25. divaricata—Madeira.
 26. juvenalis—Tunisia.

The present distribution and probable origin of all these species are discussed under the respective sections in Part II of this monograph. Here, it is only necessary to point out that the first fourteen species in the above list (through sec. 6) apparently all followed the south-Euxine route, across northern Iran and northern Asia Minor into the Balkan Peninsula, where some remained, some moved northward, and some moved farther to the west. It is very probable that their arrivals in the west were spread over a long period. *C. albida* of section 7 also followed the south-Euxine route and finally reached northern Morocco via Spain, whereas *C. achyrophoroides* probably followed the route across southern Iran and Arabia to Abyssinia. With one exception, all the species of section 8 listed here probably also followed the southern Iran-Arabian route. The one exception is *C. alpestris*, which must have taken the more northern route across Asia Minor, as did also *C. tingitana* and

C. leontodontoides of section 9. In section 10, *C. auriculaefolia* and *C. Raulini* reached Crete, probably while it was still connected with the Balkan Peninsula; *C. Triasii* and *C. oporinoides* reached southern Spain, but none of the other species in this section got farther than the Balkan Peninsula. Of those in section 11, *C. Schachtii* and *C. bithynica* reached the Balkan Peninsula, *C. tenerrima*, *C. xylorrhiza*, and *C. abyssinica* reached Abyssinia, probably by way of the southern Iran-Arabian route, and *C. Hookeriana* and *C. Faureliana* reached the Great Atlas and Saharan Atlas Mountains, respectively, either by way of southern Europe or across north Africa from Abyssinia. The probable route of *C. Reuteriana* (sec. 19) is indicated by its present distribution. In section 23 *C. patula* probably came by the south-Euxine route, through Greece, and across the land bridge to Tunisia. *C. nicaeënsis* (sec. 24) evidently came through northern Asia Minor to the Balkan Peninsula, but all the species listed from section 25, and *C. juvenalis* of section 26, probably took a more southerly route to maritime north Africa.

The second group consists of somewhat less primitive species which, because they failed for some reason to get through the Iran-Asia Minor region, remain as relics in that general region.

GROUP 2

- 5. *willemetioides*—N. Iran.
- 7. *elymaica*—W. Iran.
- 10. *Strausii*—W. Iran.
- 10. *darvasica*—Bukhara (Turkestan).
- 10. *songorica*—Alatau Mts. (Turkestan).
- 10. *sonchifolia*—E. Caucasus.
- 10. *bupleurifolia*—E. Asia Minor.
- 10. *dens-leonis*—Caucasus.
- 10. *chorassanica*—N.E. Iran.
- 10. *turcomanica*—S.W. Turkestan.
- 11. *pinnatifida*—E. Asia Minor.
- 11. *heterotricha*—Iran.
- 11. *armena*—N.E. Asia Minor.
- 11. *demavendi*—N. Iran.
- 16. *connexa*—N.W. Iran.
- 16. *sahendi*—N.W. Iran, N.E. Asia Minor.
- 16. *elbrusensis*—N. Iran.
- 16. *frigida*—central Asia Minor.

The third group contains all the rest of the species in the genus. These are obviously derived species which have developed while en route or in their present areas from species that arrived earlier. The more primitive species in this group, corresponding to the less primitive ones in the preceding groups, are shown in roman type; the more advanced species are printed in italics; and the very widespread species are indicated by bold-face type.

GROUP 3

- 8. *Schultzei*—Abyssinia.
- 8. *carbonaria*—Abyssinia and Mt. Kilimanjaro.
- 8. *Ellenbeckii*—Abyssinia, Kenya, N. Tanganyika.
- 8. *hypochaeridea*—E. half of South Africa.
- 8. *chirindica*—Mt. Chirinda (Rhodesia).
- 8. *congoensis*—Elisabethville (Belgian Congo).
- 8. *caudicalis*—Cameroon Mts.
- 8. *Newii*—Tropical Africa from E. escarpment to Angola and Nigeria.
- 8. *scaposa*—S.W. Kenya, N.E. Tanganyika, E. Congo.
- 8. *glandulosissima*—Kenya Province.
- 8. *ugandensis*—Ft. Portal (Uganda).

8. *Swynnertonii*—N. Rhodesia, N.E. Belgian Congo.
8. *simulans*—Melsetter district (S. Rhodesia).
8. *Gossweileri*—Cului (Angola).
8. *Friesii*—Ruanda (Belgian Congo).
8. *Mildbraedii*—Belgian Congo, Uganda.
8. *Bruceae*—Uluguru Mts. (Tanganyika).
9. *suberostris*—E. Algeria.
16. *purpurea*—Crimea.
19. *palaestina*—Syria, Palestine, Cyprus.
19. *pulchra*—Mediterranean region, Mid. Europe, E. to Himalaya and Tien Shan.
19. *amanica*—N. Syria.
19. *Stojanovi*—S.E. Bulgaria.
19. *pterothecoides*—S. Syria.
20. *alpina*—N.W. Iran, Transcaucasia, S. Russia, Asia Minor, Syria.
20. *syriaca*—Syria, N. Palestine.
20. *rubra*—Asia Minor, Thrace, Greece, Albania, S. Italy.
20. *foetida*—W. Iran, Asia Minor, Syria, Mid. and S. Europe to Caspian Sea.
20. *Schimperii*—Abyssinia.
20. *eritreensis*—Eritrea.
20. *Thomsonii*—N.W. India, Afghanistan, Baluchistan.
20. *Kotschyana*—Turkestan to Caspian Sea, Iran, Iraq, E. Syria.
20. *tybakiensis*—S. Crete.
22. *sancta*—Mediterranean region, and E. to N. India, Turkestan.
23. *Dioscoridis*—Greece.
23. *multiflora*—W. Asia Minor, Scarpanto, Crete, Aegean Archipelago, E. Greece.
23. *Zacintha*—Mediterranean region.
24. *capillaris*—Balkan Peninsula, Crimea-Lithuania to W. Europe.
24. *parviflora*—N. Iran, Caucasus, Asia Minor, E. Mediterranean.
24. *insignis*—W. Syria.
24. *neglecta*—N.W. Asia Minor, S. Bulgaria, N. Greece and W. to N. Italy.
24. *corymbosa*—W. Greece, S. Italy.
24. *fuliginosa*—S. Greece, E. Thessaly.
24. *cretica*—Crete.
24. *apula*—S. Italy.
24. *Suffreniana*—N.W. Italy, S. France.
25. *Noronhaea*—Porto Santo Island (Madeira Archipelago)
25. *Balliana*—Casablanca (Morocco).
25. *libyca*—N.W. Egypt, N. Libia.
25. *Claryi*—Sahara Atlas (S. Algeria).
25. *vesicaria*—Mediterranean region W. from Greece and Crete, W. Europe.
25. *Marshallii*—Caspian region, Caucasus, Crimea.
26. *aculeata*—Egypt, Palestine, Syria, Cyprus.
26. *amplexifolia*—Tripolitania, Tunisia, E. Algeria.
26. *atheniensis*—Greece.
26. *aspera*—N.E. Egypt and N.W. Arabia to N. Syria, Cyprus.
26. *setosa*—Caucasus, Asia Minor, Crimea, S. Europe to E. Spain.
26. *Muhlisi*—N.W. Asia Minor.
27. *Rueppellii*—Eritrea, Abyssinia, Kenya, Uganda, W. Sudan.
27. *Forskali*—Yemen Province, Arabia (opposite Eritrea).
27. *bellidifolia*—N.W. Italy, Tuscan Archipelago, Corsica, Sardinia.
27. *bursifolia*—Italy, Sicily; and adventive elsewhere (lawn weed).
27. *nigricans*—N. Egypt to S. Tunisia.
27. *filiformis*—Libia.
27. *senecioides*—Palestine, Sinai Peninsula, Egypt W. to S. Tunisia.

In this last group it is noteworthy that, even though almost all of the species must be considered as more advanced than other species in the genus, yet only twelve, or less than 20 per cent, are very "aggressive," widespread species. And, as might be expected, practically all of these dominant species are also polymorphic, with

well-marked geographic races or subspecies. Thus, it appears that the more advanced stages of evolution in this genus have resulted in increased speciation accompanied by special adaptation to particular sets of environmental conditions. In other words, most of these more advanced species are comparatively young endemics. Only a few have combined wide adaptability with marked specialization. It seems reasonable to associate this outcome with the evolutionary history of the group, for these species certainly developed in the Turano-Iranian-east Mediterranean region during late Pliocene and Pleistocene when great topographic and climate changes took place. In all the sections represented here, except sections 22 and 27, the species in this list are connected with more primitive allies which appear in earlier lists. *Crepis sancta* (sec. 22) appears to be related to both section 16 and section 21. Section 27 may be related to *C. tenerrima*, *C. xylorrhiza*, and *C. abyssinica* of section 11. If this is true, *C. bellidifolia* and *C. bursifolia* probably migrated from north Africa across the Tunisian-Italian land bridge before the climate of north Africa reached its extreme stage of Pleistocene desiccation.

THE BASIS OF EVOLUTION IN CREPIS

The evidence from comparative morphology, from the chromosomes, and from interspecific hybrids, as well as from geographic distribution, points definitely to the conclusion that *Crepis* is a monophyletic group of species. Excepting sections 12 and 18 and such problematical species as *C. paludosa* and $\times C. Perssonii$, the genus as a whole is not the product of intergeneric hybridization, but rather of progressive development, from a single ancestral group, of more and more advanced and specialized types. Progressive changes, morphological, physiological, and cytological, have accompanied adaptation to changing environment caused by secular changes in topography and climate and by decimation and migration. Adaptation to changing environment has been made possible primarily by the occurrence of genetic changes, both gene mutations and grosser chromosomal changes. The course of events subsequent to the occurrence of such genetic changes depended, of course, on the conditions existing in a given population. Under certain conditions natural selection must have operated in the establishment of such dominant types as the widespread xerophytic annual species like *C. parviflora* and *C. senecioides*. Under other conditions random fixation probably served to establish local endemic types, both primitive and advanced. In all, presumably, a definite balance existed between the forces of mutation pressure, selection pressure, rate of migration, and the effects of the natural method of sexual reproduction, whether largely by self- or cross-fertilization (cf. Dobzhansky, 1941, pp. 331-344).

From a synthesis of the evidence on comparative morphology, karyology, and the cytogenetics of interspecific hybrids, it has been possible to reach some definite conclusions concerning the nature of the genetic processes which have made possible the evolution of *Crepis*. Although these have been briefly discussed in chapter 1, we here set down a summary of the conclusions reached.

- 1) The **primary** genetic processes causing evolution in *Crepis* are gene mutations (see p. 12) and certain structural changes in the chromosomes.

- 2) The roles of gene mutations are the production of morphological and physiological differentiation within and between species, the accumulation of intra- and interspecific sterility, and possibly the reduction in absolute size of the chromosomes.

- 3) The roles of evolutionary chromosome changes are the genesis of intraspecific sterility leading to discontinuity and hence to speciation, and of karyotype evolution through reduction in number and symmetry of the chromosomes.

4) The **secondary** genetic processes involved in the evolution of *Crepis* are inter-specific hybridization, polyploidy, and apomixis.

5) The roles of interspecific hybridization are the augmentation of karyotype evolution and the origin of a small number of new species, especially through amphidiploidy (see Part II, sec. 15, pp. 572-616).

6) The roles of polyploidy and apomixis are a small amount of speciation, combined with extensive differentiation and geographic distribution (see especially Part II, sec. 10, pp. 416, 420; sec. 15, p. 572; and sec. 18, p. 634).

One of the most significant results of evolution in *Crepis* is the 6-5-4-3 series of haploid chromosome numbers. In this series most of the species are represented. It has been shown (Babcock and Jenkins, 1943) that all the evidence is consistent with the hypothesis that the main trend in chromosome number in *Crepis* has been a progressive decrease from a basic number of 6 to one of 3 and that this decrease took place in steps, by the loss of one chromosome at a time. Each step in decrease occurred independently of other steps and on several different occasions. It has been demonstrated in one instance (Tobgy, 1943) that the decrease from 4 chromosome pairs in *C. neglecta* to 3 pairs in *C. fuliginosa* was made possible by an unequal reciprocal translocation such that one chromosome of *C. neglecta* (or the common parent) lost nearly all of its long arm. The chromatin attached to the remaining centromere and the centromere itself are not present in *C. fuliginosa*, presumably having been lost. The loss of a chromosome, however, might also have resulted from intraspecific hybridization between two strains having translocations involving different arms of the same chromosome, namely, the one eventually lost, followed by elimination of the centromere having attached duplicated material. In either event the basic genetic process responsible for the progressive decrease from 6 to 3 pairs of chromosomes in *Crepis* is reciprocal translocation of unequal segments between nonhomologous chromosomes of individual species.

It was shown in chapter 7 that fifty-two diploid endemic species include the whole range from 6 to 3 pairs of chromosomes. The 6-paired endemics are all either primitive or intermediate in phylogenetic relations; the 5-paired ones are about equally divided among primitive, intermediate, and advanced; whereas the 4-paired species are mostly intermediate and advanced. The one 3-paired endemic (*C. fuliginosa*) is an advanced annual species. Thus, definite positive correlation exists between decrease in chromosome number and phylogenetic advancement among the endemic species, and this holds true of the diploid species in general.

That progressive reduction of chromosome numbers has been of fundamental importance in the evolution of this genus is also shown by: (1) the fact that the two species of the putative ancestral genus, *Dubyaea*, thus far examined, have a higher number ($n=8$); (2) the fact that each successive step in reduction of chromosome numbers from 6 to 3 must have occurred independently in several different species; and (3) the fact that at present the 4-paired species greatly predominate.

The antiquity of *Crepis* and the strong evidence of gradual phyletic advancement throughout the history of the genus suggest that *each step* in reduction of chromosome number may have required considerable time for its completion. It is possible, however, that there is some selective advantage in the lower number itself. Mather (1941) suggested that linkage of genes, in acting as a deterrent to free recombination of multiple genes, permits most of the individuals of a population to have the optimum combination of multiple genes without eliminating the reserve of variability which may be called upon when environmental conditions change.

By decreasing the number of linkage groups there is less opportunity for the occurrence of extreme variants and the consequent elimination of the genes determining them. These genes may be of great value to the plant under changed environmental conditions. In other words, linkage will tend to suppress extreme variants without decreasing the potential variability; and the fewer the number of linkage groups, the greater will be the suppression of these extreme variants.

However fundamental may have been this progressive reduction in chromosome numbers and the mechanical processes of chromosome alteration which made it possible, it should be remembered that these comprise only one phase of the whole process of evolution. Of equal or even greater importance is the role of gene mutations in speciation within groups having the same chromosome number (cf. frontispiece). Proof of this is found in the fact that the reduction from 5 to 4 pairs of chromosomes must have occurred at least four times in the history of the genus (see p. 69; secs. 4, 11, 14; secs. 13, 19; secs. 6, 8, 10, 23–27; and sec. 20). But these groups include at least fifty-eight and probably many more 4-paired species. This present diversity of species having the same chromosome number has come about largely through the origin and accumulation of gene mutations. The evidence from *Crepis* that gene mutations have been of primary importance in the differentiation of species has been reviewed in chapter 1 (pp. 14 and 16–20). It is only necessary to add that, whereas gene mutation is the basic type of genetic change involved in the differentiation of species having the same chromosome number, yet the gradual multiplication of species through the origin of gene mutations is a very complicated process. In the first place it is possible only when some kind of isolation exists between the differentiating populations. Furthermore, as was stated above (p. 145), the process continues only when a certain balance is maintained between various agencies or forces.

Isolation has certainly played an important role in *Crepis* speciation. Isolation capable of leading to speciation may be caused by (1) *spatial separation* or (2) *an internal mechanism*. With reference to the first category, migration of a species may be followed eventually by topographic changes which separate the original population into two or more populations. The spatial separation may remain merely geographic, or changes in the environment affecting the different populations may bring about the gradual accumulation of gene mutations causing physiological differences and thus establishing ecological isolation between them. Regarding internal mechanisms, effective isolation may be set up between certain individuals of the same population by the origin of genetic relations preventing reproduction or causing the sterility of the progeny of the two types of individuals. The various kinds of internal isolating mechanisms are classified and discussed by Dobzhansky (1941). The relative importance of these two categories of isolation in the development of new species in this group of plants cannot be summarily stated, too little being known as yet about the genetic relations between many of the species. But it is obvious that the kind of isolation which initiated speciation must have differed in different subgroups.

Whenever there was a decrease in chromosome number, effective genetic isolation was then established between the forms with unlike numbers. But this does not mean, as some authors imply, that speciation is "instantaneous." As stated above, the process of reducing the chromosome number may require considerable time. Furthermore, establishment of the new reduced chromosome number probably was not accompanied by much morphological or physiological change. It only made possible the accumulation of gene mutations which gradually built up morphological and physiological differentiation and added further genetic isolation to

that initiated by the change in chromosome number. Eventual migration or radical topographic changes have sometimes established geographic isolation among the species comprising a subgroup of closely related species.

An excellent illustration of the interaction of various factors in the evolution of a small group is found in the three very closely related species, *C. neglecta* ($n = 4$), *C. fuliginosa* ($n = 3$), and *C. cretica* ($n = 4$). It has been shown (Tobgy, 1943) that the second was derived from the first, or that the two species came from a common ancestor, primarily by reduction in chromosome number. At present *C. cretica* is morphologically very close to the other two species, but it is isolated geographically and its karyotype is distinct from that of *C. neglecta* (cf. figs. 246 and 248). For one thing, the A and D chromosomes (on extreme left and right in the figures) are definitely shorter than those of *C. neglecta*. A very plausible hypothesis concerning the phyletic relations between these three species assumes: (1) That their common 4-paired ancestor was distributed in the Balkan Peninsula in late Pliocene time. The fact that three other closely related 4-paired species, namely, *C. corymbosa*, *C. apula*, and *C. Suffreniana*, are now distributed from western Greece to southern France greatly strengthens this assumption. (2) That the earlier steps in chromosomal transformation, which resulted eventually in the 3-paired *C. fuliginosa*, probably occurred not later than early Pleistocene when Crete was still connected with the Balkan Peninsula (cf. fig. 7). These chromosome changes may have occurred in plants distributed in the now submerged region between Greece and Crete and may have been followed by southward migration of the new form destined to develop into *C. cretica*. The later submergence of this region left *C. cretica* completely isolated under increasingly arid, insular conditions, so that, through gene mutations, it has become an even more reduced species than *C. fuliginosa*. (3) That subsequent chromosomal transformations, occurring in plants restricted to southern Greece, produced the 3-paired form destined to develop, through accumulation of gene mutations, into *C. fuliginosa*. (4) That the remnant of the parental 4-paired species developed into *C. neglecta*, which is now distributed from northwestern Asia Minor through the northern Balkan Peninsula to Italy. Since all of these assumptions are consistent with the evidence from present-day distribution, comparative morphology, cytogenetics, and paleogeography, we may conclude that in this small group speciation was initiated by chromosomal transformations which led eventually to reduction in chromosome number and that the process of differentiation was augmented by the accumulation of gene mutations under the influence of migration, geographic isolation, and natural selection.

What has thus been shown to have been the probable history of one small group of species probably occurred over and over again in this genus. This follows from the conclusion, which was reached above, that the progressive decrease in basic chromosome numbers from 6 to 3 took place in steps, by the loss of one chromosome at a time, and by each step occurring independently on several different occasions.

It should be emphasized that chromosomal transformation is not the only genetic process leading to an internal mechanism causing isolation between species of *Crepis*. The investigations of a group of insular endemics and of a group of closely related widespread species (see pp. 17-18) produced evidence that gene mutations also bring about genetic isolation between closely related species which were already geographically isolated. Gene mutations have doubtless been continually at work throughout the history of this genus providing the genetic variations which made interspecific differentiation possible. But, in order that gene mutations could gradually build up effective genetic isolation, some other kind of isolation, partial at least, had to be initiated through either chromosomal transformation or migra-

tion into new environments or local environmental changes within the range of the species. In other words, gene mutation alone cannot ordinarily produce isolation between subdivisions of a species population under uniform environmental conditions if the population is either continuously distributed and sufficiently large or is subdivided into sufficiently large "islands" (Wright, 1943, p. 137). But, according to Wright (*loc. cit.*): "Even under uniform environmental conditions, random differentiation tends to create different adaptive trends in different regions and a process of intergroup selection, based on gene systems as wholes, that presents the most favorable conditions for adaptive advance of the species."

There are, however, occasional extraordinary single gene mutations which act directly in isolating species genetically. The most outstanding example in *Crepis* is the interspecific lethal gene in *C. tectorum* (see p. 14). Its discovery came from the first attempts to artificially produce hybrids of *Crepis* (Babcock and Collins, 1920; Hollingshead, 1930a). The possibility that this same gene was effective in isolating *C. tectorum* from its two closest relatives, *C. Bungei* and *C. ircutensis*, has been mentioned (see p. 14). Some evidence that similar interspecific lethals exist in other species has been noted (Hollingshead, *loc. cit.*; Babcock, 1942).

Geographic and ecologic isolation, resulting from migration, also must have played an important role in *Crepis* speciation. The importance of geographic isolation is strongly indicated by the following facts concerning the present distribution of many species, facts which may be verified from the sectional distribution maps in Part II. Of the 196 species, 75, which are found in seventeen different sections or subsections, are at present geographically isolated from all of the other species in their respective groups. These groups and the number of isolated species in each are as follows: section 4, three isolated species; 5, four; 7, three; 8A, five; 8B, five; 9, three; 10C, four; 10D, three; 10E, nine; 10F, four; 11, twelve; 13, one; 16, five; 18, one; 20, two; 21, two; 23, one; 24, one; 25, four; 26, one; 27, two. Reciprocally, there are 107 comparable species which are not completely isolated geographically, that is, species the areas of which overlap or are included within the areas of one or more of their closest relatives. This makes a total of 182 comparable species. The other 14 species consist of the 4 comprising the four monotypic sections together with the 10 American species with the basic chromosome number $x = 11$. The latter consist for the most part of polyploid complexes which make them hardly comparable with most of the species in the genus.

We find that 41 per cent of the comparable species in the genus are at present geographically isolated from their closest relatives and that 59 per cent have areas that overlap those of their closest relatives. Several sections, however, have subgroups of 2, 3, or more species the areas of which more or less overlap, but which are isolated as a group from the other species in the section. Hence the distribution maps in Part II indicate that geographic isolation has been an important factor in speciation (see, for example, figs. 131 and 184).

Although it is not nearly so apparent, it is very probable that ecologic isolation brought about through migration, either vertical or horizontal or both, into new environments has been equally important in inducing speciation. Evidence for this generalization will be found in the discussion of certain species in Part II, sections 1-6, 8, 11, 14, 19, 20, 23-25, and 27. More easily available is the evidence on endemic species (see table 8) in which 133 species are classified according to their altitude and general moisture requirements. If the present account of the history of development and migration in this genus is approximately true, it follows that ecologic isolation and accompanying specialization must have been another very important factor in *Crepis* speciation.

That there is a factual basis for the foregoing generalization becomes clear when one considers the evidence on a particular group of sympatric species (those occupying the same area). In section 19 it will be seen from figure 189 that *C. Reuteriana*, *C. palaestina*, and *C. pterothecoides* are restricted to the Syria-Palestine region and that the widespread species *C. pulchra* also occurs there. The first species mentioned is instructive in itself, since there are two well-marked subspecies. *C. Reuteriana typica* occurs at elevations from 100 to 1,900 meters and *C. Reuteriana Eigiana*, from 700 to 2,890 meters. In the mountains of Liban, where the two subspecies overlap, fertile intermediate variants occur. Evidently, subsp. *Eigiana* is much more tolerant of high altitude conditions than is subsp. *typica*; and, apparently, the overlapping areas are relatively small, although more field work is needed to establish that point. At any rate, there is partial ecologic isolation of the two subspecies, and this in course of time may become either more or less effective in differentiating the subspecies into species.

C. Reuteriana and *C. palaestina* have both been collected in the Ehden district in Liban. Whether they occur together in other areas and whether they actually grow near one another in the Ehden district is not known; but no intermediate variants have been seen by me. Hybridization experiments between these two species have not been made. It is not unlikely, however, that F_1 hybrids are fully as sterile as hybrids between *C. Reuteriana* and *C. pulchra* (see below). If this is true, their isolation in nature is due to an internal mechanism.

C. pulchra, according to the descriptions given in floras, has been reported from the Liban region in the form of subsp. *typica*. If it comes in contact with *C. Reuteriana*, it would probably be with subsp. *typica*. First generation hybrids between *C. Reuteriana typica* and *C. pulchra typica* were only 3 or 4 per cent fertile. Hence, they are well isolated by an internal mechanism. On the other hand, F_1 hybrids between *C. pulchra typica* and *C. palaestina* are 30 to 50 per cent fertile, and the F_2 progeny are vigorous and more or less fertile. So far as is known, however, the two species do not hybridize in nature. Apparently, they either do not occur together or, if they do, they do not flower at the same time. Also, *C. pulchra* is definitely a xerophyte, whereas *C. palaestina* is much more mesophytic. Finally, *C. pulchra* enters only the northern part of the area occupied by *C. palaestina*, and in the overlapping region they are apparently isolated ecologically, although difference in season of flowering may be an important factor.

C. pulchra is also genetically close to *C. pterothecoides*. Although controlled hybrids have not been made, the two species were found to have crossed in the greenhouse and the hybrids were highly fertile. *C. pterothecoides* is an even more strongly xerophytic species than *C. pulchra* and is correspondingly more advanced or specialized morphologically and physiologically. Since *C. pulchra* occurs sporadically in central Syria, it is possible that plants of the two species might sometimes occur together. But natural hybrids would be very unlikely to occur because *C. pterothecoides* is very precocious in time of flowering and, under desert conditions, the flowering period would be short, whereas *C. pulchra* is slow in developing to the flowering stage. This marked physiological difference would serve as an effective isolating mechanism.

The above illustration serves to emphasize the complicated nature of the isolating factors which separate closely related sympatric natural species. Our present knowledge of this genus is too incomplete to make possible a more definite statement concerning the nature of the isolation of other sympatric species of *Crepis*. But the known or strongly indicated relations between the members of this one group will serve at least to indicate the nature of the isolating factors in other groups of closely

related species the areas of which more or less overlap one another. It is certain that ecological specialization has played an important role; but other kinds of genetic differentiation, such as difference in flowering season, have also been important.

Stebbins (1942*b*), in discussing the role of isolation in the differentiation of plant species, has advanced the hypothesis that internal isolating mechanisms evolve gradually and are genetically independent of the morphological changes which produce visibly different species. Clausen, Keck, and Hiesey (1945) also emphasize the *gradual* development of such isolating mechanisms. Although supporting experimental evidence is not available in *Crepis*, the history of the genus, as recorded in this monograph, cannot fail to give the impression that the evolution of this group has been a slow, gradual process.

The tempo of evolution, however, has not been uniform among the species comprising this genus. In fact, the general picture resembles that portrayed for the Carnivora and the Pelecypoda by Simpson (1944, p. 128) in that only a few of the existing species of *Crepis* can be considered to have originated in early Tertiary, whereas a large proportion of them must have had their origin during Pliocene-Pleistocene (see pp. 139–141). Thus, the evidence from *Crepis* indicates that this genus includes at least two types of species with reference to their tempo of evolution: (1) the few most primitive species in the genus which have changed very little since early Tertiary; and (2) the many more advanced intermediate species and the most advanced species, all of which have probably evolved since mid-Pliocene.

The extreme contrasts between oldest and youngest species in this genus (for example, *C. sibirica* and *C. suberosa* or *C. conyzaeifolia* and *C. senecioides*) can be harmonized by the conception that the extremes are actually connected by extensive series of intermediate types. Many of these intermediate species still exist, but many others have doubtless become extinct. A large proportion of those which still exist are endemic relics which occur in restricted areas presumably because of their definitely limited tolerance to environmental variations. Most of the youngest species in the genus are also endemics which appear to be restricted in distribution because, along with their specialization, they have become adapted to particular sets of environmental conditions; whereas only a dozen or so combine high specialization and wide adaptability (see p. 144).

In general, adaptation in *Crepis* involves physiological changes which are correlated with progressive morphological changes and reduction in chromosome number. The most important adaptive trend in the genus includes those changes which accompanied the persistence of old species and speciation under increasingly xeric conditions. Outstanding among these changes are: (1) development of the deep taproot from the rhizome; (2) development of the biennial, the annual, and the precocious annual from the perennial life cycle; (3) reduction in size of the plant and its parts; (4) increased specialization for seed distribution by the wind, including increase in number and reduction in size of the flower heads, thickening and reflexing of the inner involucre bracts, decrease in size and weight of achenes, and development of a slender beak on the achenes; and (5) increase in length of viability of the seeds, as in *C. capillaris* and *C. senecioides*.

Certain species of *Crepis* have also developed various special adaptations. For example, the most characteristic change accompanying adaptation to high alpine conditions is development of the low, tufted habit of the plant (*C. terglouensis*, *C. nana*). The ability of *Crepis pygmaea* and *C. nana* to colonize steep, gravelly slopes resulted from the development of stolonlike underground shoots. In *Crepis natula* and *C. Zacintha* extreme induration of the involucre results in enclosing the achenes until the involucre disintegrates. In the last two species this particular

modification may make possible the distribution of the seeds by streams. In *Crepis Clausonis* and *C. vesicaria* subsp. *hyemalis*, the strictly winter-blooming habit seems to be a special adaptation to seasonal moisture.

Regardless of any doubts concerning the validity of the special adaptations listed above, the general importance of the morphological and physiological changes

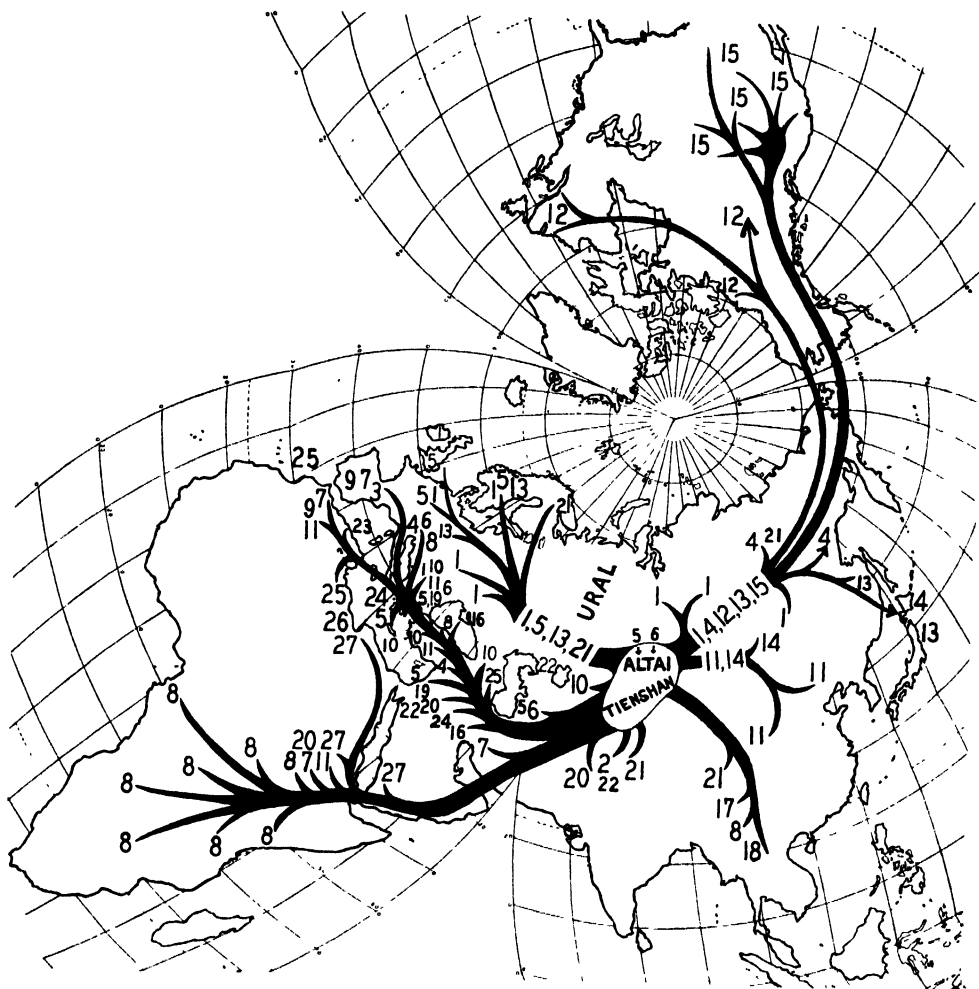


Fig. 11. Diagrammatic representation of the principal migration routes of *Crepis* from the assumed center of origin in Central Asia. The numbers designate the sections. From the Altai region, sections 1, 5, 13, and 21 moved westward, and sections 1, 4, 11, 12, 13, 14, 15, and 21 moved northeastward and eastward. From the Tien Shan region, sections 8 (one species), 17, 18, and 21 moved southeastward, and all the other sections or their progenitors moved southward and south-westward. Based on Goode Base Map No. 201 PC. By permission of the University of Chicago Press.

that have accompanied adaptation to an increasing desiccation of the climate cannot be doubted. All of these adaptations appear to have developed gradually through the accumulation of minor genetic changes.

The evolution of *Crepis* has depended primarily upon two general categories of genetic change: (1) gene mutations and (2) reciprocal translocations between nonhomologous chromosomes. But the evolution of *Crepis* has involved adaptations

to almost every type of environmental change to which flowering plants have been subjected throughout their long development. These adaptations have come about, presumably, not only through natural selection but, in some species, through limitation of population size, which has resulted in random fixation or genetic drift (gene spread). The forces of natural selection, random fixation, and gene spread have been brought into play partly through the migration of species into new environments and partly through secular or catastrophic changes in topography and climate. Spatial isolation of populations, resulting from any of the above conditions, has been of paramount importance in the development of new species. And the reuniting of more or less differentiated populations through migration has apparently been important in developing such polymorphic superspecies as *C. foetida* and *C. vesicaria*. Genetic isolation, induced by such an internal mechanism as that set up by the process leading to reduction in chromosome number, has also played an important role in *Crepis* speciation. But equally important in the multiplication of species with the same chromosome number is the differentiation, both morphological and physiological and including other internal isolating mechanisms, which has been brought about through the gradual accumulation of gene mutations. The development of those other internal isolating mechanisms, such as difference in flowering season and genetic incompatibility or hybrid sterility due to genic divergence, probably depended on some kind of spatial isolation for the conditions essential for their development (see Dobzhansky, 1941, pp. 280–288).

The results of evolution in this genus are epitomized by the contrast between the oldest and youngest species. The most primitive *Crepis* species are robust, rhizomatous, mesophytic perennials with large simple fruits and short-lived seeds. The highest culmination of the long history of the group is found in the small, delicate desert annuals, with their extreme precocity, ephemeral fibrous taproot, tiny fruits with a filamentous beak, and seeds of longer viability.

It may be well, in conclusion, to repeat that the basis of taxonomic classification in this work consists of morphological and chromosomal resemblances and differences, supplemented by evidence from ecology, genetics, and cytogenetics. Along with this evidence, it was possible to use the evidence from geographic distribution in constructing a hypothetical scheme of phylogenetic relations between the sections, and between *Crepis* and its putative ancestors, which was found to be consistent with the limited fossil record of *Crepis* and with a great mass of paleobotanical and floristic evidence on the development and migration of floras in Eurasia, North America, and Africa. The consistency of this evidence on phylogeny and geographic distribution warrants the derivation of conclusions pertaining to evolutionary processes in *Crepis* which are of general significance.

SUMMARY

This account of the origin and migrations of *Crepis* is summarized diagrammatically in figure 11, which indicates the probable center of origin, the general direction of the four migration routes, and, roughly, the distribution of the twenty-seven sections. The center of origin and the migration routes have been assumed on the basis of the following:

- 1) Evidence from morphologic, karyologic, and genetic resemblance, indicating that the genus is essentially monophyletic.

- 2) Evidence from the present distribution of closely related genera and of the more primitive sections of *Crepis* which, considered as a whole, certainly indicates radiation from an Asiatic center along the four main migration routes assumed for *Crepis*.

3) Evidence from geology that the Altai-Tien Shan region was an available and suitable environment for the development of *Crepis* during the Tertiary period; that the great mountain axis to the south was of later origin; that the Beringian land bridge was available for the migration of the progenitors of section 15 and one species of section 12 into North America; and that the gradual desiccation of the Obic and Tethys seas during the first half of the Tertiary period, followed by gradual lowering of the temperature during the second half, provided conditions favoring the westerly and southerly trends of migration.

4) Evidence from paleobotany indicating that the Altai-Tien Shan region was part of a Tertiary floristic province in which *Crepis* could have flourished; and that many species of woody plants, including *Cedrus*, *Datisca*, and *Fagus*, were distributed to the east, south, and west from that general region in the Tertiary period.

5) Evidence from the present distribution of many genera of plants, including some in the Crepidinae, particularly *Taraxacum*, indicating a similar history to that of *Crepis*.

6) Evidence from endemism which is of outstanding importance in this genus. More than 70 per cent of the species are endemic, including some of the most primitive and some of the most advanced species. The primitive endemics are relics, being the present-day representatives of ancestral species which were widely distributed in Miocene-Pliocene. These primitive relics of restricted distribution were able to survive the severe climatic fluctuations of the Pleistocene epoch by becoming adapted to the special niches which they now occupy. The advanced species of the Mediterranean region, including the littoral endemics, were also derived from ancestors, some of which were probably distributed from Central Asia to the shores of the Atlantic Ocean in late Pliocene and early Pleistocene. During the most severe periods of desiccation they became adapted to the special conditions existing in the regions or localities where they now occur.

7) The numerous secular changes in topography and climate which occurred throughout southern Eurasia and northern Africa, especially during the latter half of the Tertiary and the Quaternary periods, provided suitable conditions for the development of new types, especially for progressive evolution toward the annual xerophytic type. These changes also caused the restricted distribution of many species.

8) The evolution of more and more advanced types of *Crepis* species from a single ancestral group has been made possible, primarily, by the occurrence of gene mutations (see p. 12), together with such structural changes in the chromosomes as may lead to genetic isolation, and, secondarily, by interspecific hybridization, polyploidy, and apomixis.

9) Speciation in *Crepis* depends not only upon the origin of new genetic changes but also upon the occurrence of some kind of isolation which prevents the differentiating populations from interbreeding. Gene mutations are essential for differentiation, but they cannot induce speciation in the absence of some kind of isolation, either spatial isolation (geographic or ecologic) or isolation due to an internal mechanism. Chromosome alterations leading to reduction in chromosome number initiate isolation; and this type of genetic isolation is of primary importance in *Crepis*, since most of the species are diploid and they comprise a progressively reducing series of haploid chromosome numbers from 6 to 3. Gene mutations can develop a type of genetic isolation between two populations only if the populations are already isolated in some other way.

10) The new biotypes produced by fortuitous genetic changes are assumed to have been subjected to natural selection and to any of the changing genetic condi-

tions resulting from migration, from decrease and increase in size of population, and from spatial isolation and reunion of populations.

11) Adaptation to gradually increasing xeric conditions has been of special importance in the evolution of this genus. The morphological and physiological changes making this adaptation possible have been part of the general process of differentiation through gene mutations under the influence of natural selection.

APPENDIX 1

SOME CREPIS PROBLEMS CALLING FOR FURTHER RESEARCH

THE PRESENT AUTHOR is keenly aware of the numerous problems connected with the origin and evolution of the genus *Crepis* which require further research for their solution. It is his hope that by calling attention to some of them there will be a better chance of their receiving consideration on the part of other scientists, especially of botanists situated in or near those countries where the various problems can be most conveniently attacked.

INTERGENERIC RELATIONS

Crepis and Dubyaea.—That *Crepis* and all the other genera of subtribe Crepidinae originated from the genus *Dubyaea* when that group was much larger and more widely distributed than it is at present seems to be a safe assumption (cf. pp. 62–65). But a gap exists in the chromosome number of *Dubyaea* and those of *Crepis*. Except for the obviously derived groups of *Crepis* (sec. 12, *Ixeridopsis* ($n = 7$), sec. 15, *Psilochaenia* ($x = 11$), and possibly sec. 18, *Pyrinachos*, in which no chromosome studies have yet been made), the highest haploid or basic number is 6. In *Dubyaea*, on the other hand, the lowest known number is 8. It was necessary, therefore, to assume that *Dubyaea* or primitive *Crepis* species existed in the past, if not now, with the haploid number 7. In section 12, *Ixeridopsis*, it was also necessary to assume that *Crepis* species, or *Crepis*-like *Dubyaea* species, once existed with the haploid number 7 (cf. p. 65); and that these hybridized with certain *Ixeris* species, or *Ixeris*-like *Dubyaea* species, also with the number 7 (cf. p. 70).

Up to the present, only two species of *Dubyaea*, namely, *D. oligocephala* and *D. hispida*, have been examined cytologically. It would be highly desirable, therefore, that all the other known species of *Dubyaea* be obtained in living condition and be studied, cytologically at least. Hybridization experiments with all of these *Dubyaea* species and the most primitive species of *Crepis*, followed by cytogenetic research on such hybrids as could be obtained, would of course be equally desirable. The technical difficulties of rearing these primitive species are considerable, but they are probably not insurmountable, even though special techniques are likely to be required. For example, in working with high alpine species at stations situated at low elevations, it has been found advantageous to sow the seeds in flats and to transport them to higher elevations where they will be exposed to the elements during winter and spring. It is important that they be covered with snow during winter and that they be subjected to alternate freezing and thawing in the early spring. It is probable that an artificial setup simulating these natural conditions could be devised. Still more certain and satisfactory would be the culture of the plants from living roots brought to the experimental station from their natural locations. During the summer of 1930 the author himself collected living roots of nine perennial species of *Crepis* in the Mediterranean region, some of which were high alpine plants, and sent them by ordinary post (not by airplane) via Washington to California without the loss of a single species. He has never been able to obtain living roots of any Asiatic species; but with adequate preparation for their collection and preservation it should be possible at least to examine the chromosomes of these Asiatic alpine species. The desirability of thorough exploration for additional primitive *Crepis* and *Dubyaea* species in Asia is discussed below under distributional problems.

Crepis and *Youngia*.—The problem of the true generic status of *Youngia tenuifolia* (Willd.) Babc. et Stebbins (Carnegie Inst. Wash. Publ. No. 484: 46–59, 1937) is still somewhat in doubt. To be more precise, one should say that it is the *exact origin* of this polymorphic, polyploid, and partially apomictic complex of forms which is in doubt. Probably it is more satisfactorily disposed of by keeping it in the genus *Youngia* than by transferring it back to *Crepis*. At any rate, before restoring it to *Crepis* all angles of the problem should be very carefully considered, and efforts should be made to obtain more factual data bearing on its origin.

It was pointed out by Babcock and Stebbins (*op. cit.*, p. 59) that, in order to account for the morphological characteristics of all of the polyploid forms comprising *Y. tenuifolia*, it is necessary to assume the existence, now or earlier, of at least three different diploid ancestors. One of these assumed diploids would represent the foundation stock of subsp. *typica*, another subsp. *altaica*, and the third must have been involved in the origin of subsp. *diversifolia*. The geographic distributions of the three subspecies are as follows: *typica*, in S. Siberia from Irkutsk to Nertchinsk Provinces and south to N. Manchuria and Mongolia; *altaica*, in the S.W. Altai region; *diversifolia*, from the Altai Mts. through the mountains of Turkestan and W. Tibet to the Himalayan region. Thus two of the assumed diploids might be expected to occur in Central Asia, but diploid *typica* would probably have to be looked for farther to the east.

Babcock and Stebbins (*loc. cit.*) also state: "The phyletic relations of the diploid subspecies with other species of *Youngia* are more obscure. Too little is actually known about chromosome number and morphology in this genus to warrant any hypothesis based on cytological evidence. If the diploid subspecies of *Y. tenuifolia* are 5-paired, one could assume that they represent a connecting link between *Youngia* and *Crepis*, a hypothesis supported by their morphological characteristics."

Searching for these assumed diploid forms of *Y. tenuifolia*, therefore, is to be encouraged, not only with the object of learning more about the nature and origin of this interesting heteroploid complex (see Babcock and Stebbins, 1938, pp. 58–69), but also because such investigation may throw more light on the relationship between *Youngia* and *Crepis*. It is hoped that botanists of the U. S. S. R. will take a special interest in these problems.

Crepis and *Ixeris*.—The probability that section 12, *Ixeridopsis*, originated through hybridization between *Crepis* species and *Ixeris* species with $n = 7$ chromosomes, or between two *Dubyaea* species which had already become *Crepis*-like and *Ixeris*-like, was mentioned above. Cytogenetic experiments with attempted hybrids between *Ixeris alpicola* and any available species of section *Ixeridopsis* might throw some light on this interesting problem.

Crepis and *Hieracium*.—The possibility that *Crepis paludosa* originated through hybridization between *Crepis* and *Hieracium* before these two genera were as strongly differentiated as at present (cf. Part II, p. 236) might be investigated by cytogenetic research on hybrids between *C. paludosa* and various *Hieracium* species, for example, *H. Knuthianum* (cf. Pax, 1898, p. 32).

MORPHOGENETIC PROBLEMS

Plant form and phylogeny.—Raunkiaer (1937, p. 42) asserts that the "Proto-Hemicyptophytes pass imperceptibly into the Suffruticose Chamaephytes, from which most of them are certainly descended." All the species recognized as most primitive in *Crepis* are Hemicyptophytes. They have a rhizome and 6 pairs of chromosomes. The few suffruticose or suffruticulose species in this genus all have deeply penetrating taproot and less than 6 pairs of chromosomes. Is this actually

an exception to the generalization of Raunkiaer? Or should one after all assume that, even in *Dubyaea*, the deeply penetrating root and suffruticose habit was more primitive and that the corresponding species of *Crepis* were derived from such ancestors? This latter assumption would require the recognition of a still greater gap in chromosome numbers than now exists between *Crepis* and *Dubyaea*, unless, indeed, one of the existing species of *Dubyaea* with a taproot should turn out to have 7 or 6 pairs of chromosomes. On the basis of this assumption it would follow that the rhizomatous species of *Dubyaea* and *Crepis* are derived forms which have become adapted to a very moist habitat. Because of the evidence within *Crepis* indicating that several species characterized by a taproot were derived from rhizomatous species (for example, sec. 14 derived from sec. 4, and sec. 19 from sec. 13), my assumption that the most primitive species of *Crepis* (and probably of *Dubyaea*) were rhizomatous seems probable. But it is equally probable that the most primitive species of *Dubyaea* were taprooted. Attention is called to this problem in order to emphasize the desirability of research on the phylogenetic relations between these two types of species in both these genera; and this further emphasizes the importance of future exploration in Central Asia for additional species of both genera.

Crepis rhaetica of section 4 offers especially promising material for an ontogenetic investigation of development of the underground part of the plant. No question exists about the subcaudical part being a rhizome, since a comparison of its gross histology proves that it is closely similar to that of *C. sibirica* and *C. kashmirica*. With the help of Dr. Adriance S. Foster, pieces of rhizomes of these three species were bleached and cleared sufficiently to reveal their gross structure.¹ In *C. sibirica* and *C. kashmirica* the vascular system has the aspect of a typical dictyostele. When a piece of the rhizome is split longitudinally each piece contains a half-cylinder of yellow woody tissue. Inside the cylinder is the pearly white parenchymatous tissue of the pith, and outside of it is the cortical tissue. Every lateral root could be seen to contain a central vascular strand which branched off from the stele. The rhizome of *C. rhaetica* is closely similar to those of *C. sibirica* and *C. kashmirica*, except that the stele is not composed of so many vascular fibers, which fibers could be seen to be interlaced. Since lateral root fibers arise in the same way as in the other two species, there can thus be no question about these species being rhizomatous.

C. rhaetica, however, in that its rhizome apparently has a growing point at each end, presents a special problem, which is taken up in Part II, p. 254, and figure 24. Unfortunately, in all the herbarium material thus far examined, the lower growing point could not be demonstrated and it is assumed to have been broken off. It would certainly be of interest to grow a considerable number of seedlings of this species so as to make examinations at successive periods in ontogeny. This should establish beyond any question the method of downward elongation of the rhizome in this species. Such a study would also provide valuable evidence on the relation between the rhizome and the hypocotyl, and should answer the query whether the seedling of a rhizomatous species first produces a true root which aborts after the rhizome begins to develop. If this should be found to be the typical ontogenetic behavior in rhizomatous species, it would be an argument in favor of considering the taproot more primitive than the rhizome. All the phylogenetic evidence within *Crepis* points to the opposite conclusion, but this does not invalidate the assumption that the more distant ancestors of *Crepis* were taprooted.

Observations on the development of the root system in young seedlings of four

¹ Following are the essential steps in the process: (1) heat in water for an hour or less; (2) transfer to 5 per cent sodium hydroxide and place in oven at 52–53° C. for two or three days; (3) wash in water, dehydrate in ethyl alcohol, and examine in alcohol under the dissecting microscope.

species of *Crepis* certainly indicate that the taproot is a more primitive feature than the rhizome. The first of these species is *C. hierosolymitana*, one of the few rhizomatous species of which viable seed was available. The second of these four is *C. Reuteriana* subsp. *Eigiana*, which, from herbarium specimens, is known to develop a strong woody subterranean stem and which has therefore been considered an intermediate type between the rhizomatous and the taprooted types. The other two species are *C. scaposa* subsp. *taraxaciformis*, a perennial, and *C. pulchra*, an annual, both being taprooted. With the assistance of Mrs. Ruby Allen Valencia, seeds of these four species were germinated and cultured individually in pots under uniform conditions and studied histologically in their earlier stages of development.

C. hierosolymitana. All the seedlings developed a primary root which developed as a taproot with many branches. Cross sections of the main root taken just below the caudex showed an arrangement of xylem elements which is typical of root structure. It is clear that the rhizome must develop later in ontogeny; and apparently it develops from the caudex and is accompanied by the appearance of adventitious roots.

C. Reuteriana. The seedlings developed a primary root which continued to develop as a taproot to the end of the period of study. At that time all cross sections of the taproot showed the typical central stele characteristic of root structure. Sixteen months later (June, 1946), after these seedlings had flowered twice, it was found that the caudex was about 2 cm long, the upper half being a rhizome about 6 mm in diameter, with typical stem structure and small lateral roots; and the lower half, about twice as thick, was intermediate in structure, bearing large lateral roots and tapering into the strong taproot. Hence, it may be inferred that the underground stems, seen in certain herbarium specimens, developed by annual increments about 1 cm in length and that such specimens must be at least 9 or 10 years old. It is evident that, in this species, the caudex begins to develop as a rhizome in the second year. The strong roots at the base of the caudex are adequate to support the plant for years, and the small lateral roots of the rhizome may disappear completely, giving it the appearance of an underground stem.

C. scaposa and *C. pulchra*. As was to be expected, seedlings of both of these species developed a taproot which continued to grow throughout the period of study.

The evidence is clear that the hypocotyl develops into a root in all four species. For this reason the root must be considered a more primitive structure than the rhizome. This is consistent with the hypothesis that the rhizome is merely a modified caudex with adventitious roots and that it was evolved as an adaptation of a taprooted type to a moist environment.

The genetic basis of root versus rhizome.—This is another phase of the foregoing general problem which the present author has not been able to study in the progeny of interspecific crosses. It is very desirable that this be done. But it is practically essential that such work be attempted at a station where the wild species themselves will thrive and develop their characteristic subterranean parts. This probably calls for garden cultures under conditions simulating as nearly as possible the natural habitats of the wild species. In this connection there should also be conducted some transplantation experiments from the natural habitats to conditions less and less natural for each species in order to ascertain the degree of direct modifiability in type of root which is latent within each species.

The genetic basis of beaked achenes.—Such crosses as have been made between species of *Crepis* with beaked and unbeaked achenes indicate that the beak is the result of the accumulation of numerous minor mutations. It is very desirable, however, that this question be investigated further by first finding two species,

one with long beaked and the other with shortly beaked or unbeaked fruits, which will produce hybrids with sufficient fertility to make possible a large-sized second generation.

DISTRIBUTIONAL PROBLEMS

The need of exploration for additional species.—That *Dubyaea* species may exist in Central Asia is an interesting possibility. The fact that one species of *Sorosseris* is known from Tien Shan seems to increase the likelihood of such a discovery. Furthermore, a 7-paired *Dubyaea* would strengthen our hypothesis about the origin of *Crepis* (see p. 65). It is hoped that botanical collectors will keep this desideratum in mind. Search should also be made, probably in the eastern Tien Shan and Dzungaria regions or perhaps also in eastern Altai, for the diploid forms of *Youngia tenuifolia*. The possibility that other species of *Ixeris* than *I. alpicola* were involved in the origin of section 12, *Ixeridopsis*, and that such species of *Ixeris* may still exist in Central Asia should be kept in mind. The possibility also exists that primitive, relic, alpine species of *Hieracium*, having close relatives in Europe, may yet be found in Central Asia. That such species are completely absent from that region, as well as from the arctic regions and from Scandinavia, was accepted by Engler (1879, p. 131) as evidence that the alpine *Hieracia* of southern Europe (Pyrenees, Alps, Carpathians, Balkan Peninsula) developed since the glaciation of Europe. But this does not preclude the possibility that their ancestors migrated from Central Asia into southern Europe over the same southwesterly route that *Crepis* followed. Engler finds it necessary to assume that *Hieracium alpinum* existed during the Glacial epoch and was able to migrate from the Alps to Sudeten, Harz, Scandinavia, Karisch Gulf, Greenland, and other parts of arctic America. But most of these alpine *Hieracia* are assumed to have arrived from Central Asia too late to be able to cross the European lowland to the north of the Alps. If they or their ancestors actually did migrate from Central Asia, it would seem likely that sooner or later some traces of these relics would be discovered along the route or in the assumed region of origin.

Distribution in Crepis Dioscoridis.—An interesting distributional problem is presented in connection with the question concerning the real nature of the forms recognized as subspecies (cf. Part II, pp. 746–757). Three of the four subspecies of *Crepis Dioscoridis* are known from very scanty material and each from only a single locality. Thorough field studies are needed and should be supplemented by garden cultures designed to test the amount of natural hybridization going on. Since all three of these subspecies occur within the geographic area of subsp. *typica*, it would seem that they may be isolated from the latter, to some extent at least, either ecologically, seasonally, or by internal mechanisms.

Distribution in Crepis neglecta.—Similar problems exist with respect to *Crepis neglecta* and some of the species most closely related to it. Although it is known that an effective isolating mechanism exists with respect to *C. fuliginosa* of southern Greece and eastern Thessaly, it would be desirable to ascertain the exact southern limits of *C. neglecta* in Greece and the amount of intergradation between the two species along this boundary. The relation between *C. corymbosa* and *C. fuliginosa* is similar, since the two may meet in northwestern Greece or the adjacent islands. Whether *C. corymbosa* and *C. neglecta* contact each other is not known, but it is certain that *C. corymbosa* occurs in the area of southern Italy occupied by *C. apula*, where the two species seem to be well isolated by their different flowering seasons. *Crepis neglecta* also occurs in southern Italy, but it may be isolated from *C. apula* in the same way. Additional investigations on these species and the relationships between them are certainly desirable.

Distribution of the subspecies of Crepis albida.—Another problem worthy of thorough investigation is that concerning the distribution and degree of isolation of the several subspecies of *Crepis albida*. Although several have previously been recognized as species, yet some evidence of intergradation exists, at least between a few of them; furthermore, *C. albida Grosii* is an extremely variable complex of forms. Two of these subspecies have been found to grow well and to produce abundant seed in the experimental garden. It is very desirable that they all be brought together for comparison, experimental crossing, and cytological study, and that adequate field studies be made of their distribution and variation.

A number of other *Crepis* species need investigation concerning the actual nature of their subspecific forms, both distributionally and genetically. Among these may be mentioned especially: *C. sibirica*, *C. paludosa*, *C. pygmaea*, *C. aurea*, *C. conyzaeifolia*, *C. achyrophoroides*, *C. aurea*, *C. hypochaeridea*, *C. Newii*, *C. scaposa*, *C. suberostris*, *C. biennis*, *C. bupleurifolia*, *C. oreades*, *C. heterotricha*, *C. armena*, *C. Reuteriana*, *C. palaestina*, *C. pulchra*, *C. Bodinieri*, *C. rigescens*, *C. lignea*, *C. alpina*, *C. foetida*, *C. sancta*, *C. capillaris*, *C. Bourgeauii*, *C. vesicaria*, *C. aspera*, *C. setosa*, and *C. Rueppellii*. Also, several species known only from the type locality deserve special attention with respect to their present size and distribution. Arranged by regions, these are: Balkan Peninsula and Crete: *C. Guioliana*, *C. Schachtii*, *C. tybakiensis*, and *C. Atheniensis*. Asia Minor and Syria: *C. albiflora*, *C. khorassanica*, *C. amanica*, *C. insignis*, and *C. Muhlisii*. Central Asia and Iran: *C. darvasica* and *C. demavendi*. Southeastern Asia: *C. chloroclada*. Africa, northern: *C. Faureliana*, *C. Fontiana*, *C. Balliana*, and *C. Claryi*. Africa, tropical and southern: *C. suffruticosa*, *C. urundica*, *C. chirindica*, *C. congoensis*, *C. ugandensis*, *C. simulans*, *C. Gossweileri*, *C. Friesii*, and *C. Bruceae*.

The species which have not yet been investigated cytologically or genetically but which, in order to round out the evidence from the chromosomes as well as geographic distribution, should at least have their chromosomes examined, listed by sections, are: (4) *C. dioritica*. (5) *C. smyrnaea*. (6) *C. rhaetica*. (7) *C. achyrophoroides* and *C. elymaitica*. (8) *C. keniensis*, *C. iringensis*, *C. meruensis*, *C. cameroonica*, *C. Schultzei*, *C. carbonaria*, *C. Ellenbeckii*, *C. urundica*, *C. chirindica*, *C. congoensis*, *C. caudicalis*, *C. glandulosissima*, *C. ugandensis*, *C. Swynnertonii*, *C. subscaposa*, *C. simulans*, *C. Gossweileri*, *C. Friesii*, *C. Mildbraedii*, and *C. Bruceae*. (10) *C. Strausii*, *C. darvasica*, *C. songorica*, *C. sonchifolia*, *C. bertisceae*, *C. bupleurifolia*, *C. albanica*, *C. macropus*, *C. dens-leonis*, *C. Sibthorpiana*, *C. khorassanica*, *C. auriculataefolia*, *C. turcica*, *C. Pantocsekii*, *C. turcomanica*, *C. Guioliana*, *C. crocifolia*, and *C. athoa*. (11) *C. pinnatifida*, *C. tenerrima*, *C. xylorrhiza*, *C. Faureliana*, *C. heterotricha*, *C. armena*, *C. demavendi*, and *C. abyssinica*. (12) *C. corniculata*, *C. alaica*, *C. lactea*, and *C. naniforma*. (14) *C. ircutensis*. (16) *C. conneza*, *C. sahendi*, *C. purpurea*, *C. elbrusensis*, and *C. frigida*. (17) *C. napifera*. (18) *C. Phoenix*, *C. Bodinieri*, *C. rigescens*, *C. lignea*, and *C. chloroclada*. (19) *C. amanica*. (20) *C. tybakiensis*. (21) *C. tibetica*, *C. Gmelini*, and *C. elongata*. (24) *C. insignis*. (25) *C. spathulata*, *C. Salzmannii*, *C. Balliana*, and *C. Claryi*. (26) *C. atheniensis* and *C. Muhlisii*. (27) *C. Rueppellii*, *C. Forskalii*, and *C. filiformis*.

The genetic nature of narrow endemics in Crepis.—In connection with distributional problems, mention should be made of the interesting questions connected with population dynamics. These questions, of course, involve genetic relations rather than merely distributional ones; but the facts of distribution in nature certainly have a direct bearing on the nature of the population. For example, in chapter 7 (pp. 128–129) is given a brief discussion of the nature of narrow endemic species in *Crepis* which is based on those few species concerning which enough is

known to warrant the assumption that they are of very narrow distribution. Even so, for these few species and others, more definite information concerning distribution and variability is greatly to be desired. The present author believes that *Crepis* offers many attractive opportunities for profitable studies on population dynamics.

EVOLUTIONARY PROBLEMS

Interspecific lethal genes.—The first of the two generally important evolutionary problems of a genetic nature, which certainly deserve consideration from students who are planning future investigations in experimental evolution, is that concerning the generality of occurrence of interspecific lethal genes in *Crepis* and the true nature of the roles they have played in speciation. After the discovery by Hollingshead (1930a) of an interspecific lethal in *Crepis tectorum*, causing the early death of hybrids with *C. capillaris*, it was the hope of the present author that a comprehensive search for such lethals could be made among many species of *Crepis*. A systematic effort to this end has not been possible, although certain incidental data seemed to indicate that such genes may exist in other *Crepis* species. In order to make such a systematic research, a large collection of species in living condition must be accumulated and maintained for a period of years. This in itself is an expensive undertaking. Unfortunately, it has not been possible to preserve in living condition many of the species which were once under cultivation at the University of California. It will require years to build up another such collection even after war conditions are sufficiently ameliorated to allow it being done. But sometime, somewhere, such a collection should once more be brought together. Then, this research for interspecific lethals and many other genetic and cytogenetic problems can be worked out.

Meanwhile, we are faced with one particular problem of a kind which I hope some Russian geneticist will be able to solve. If the interspecific lethal in *Crepis tectorum* actually was of evolutionary significance, it should have functioned in isolating this species from its two nearest relatives, *C. Bungei* and *C. ircutensis*. Experimental hybrids between *C. tectorum* and *C. Bungei* have not been made; and *C. ircutensis* has never been brought into cultivation. It would be very desirable to bring these three species together under controlled conditions and to make experimental crosses using numerous individuals of each species for the purpose of finding different genotypes with reference to the lethal gene.

Self-incompatibility.—The second problem of general evolutionary significance is that concerning the genetic basis of self-incompatibility in *Crepis*. Although many species, like *C. tectorum* and *C. pulchra*, are highly self-fertile, many others are more or less self-sterile. This has been shown by Hughes (1943) in *Crepis foetida* subsp. *rhoeadifolia* to be due to self-incompatibility of the pollen. Cytological studies have shown that a plant's own pollen usually fails to germinate, and in the rare instances when it does germinate it fails to penetrate the stigmatic surface. Among the material available, four intrasterile groups were discovered, some of which were also intersterile. From the data on three generations of crosses, we may make certain assumptions concerning the genetic basis of self-sterility in this subspecies. One major set of alleles is responsible for the self- and cross-sterilities. They are designated S_1 , S_2 , S_3 , and S_4 . It is postulated that (1) Pollen behavior is sporophytically determined. That is, the behavior of a pollen grain is dependent upon the genotype of its parental sporophyte. (2) S_1 is recessive to all three of the other alleles. S_2 is dominant to S_1 , but recessive to S_3 and S_4 ; whereas S_3 and S_4 are both dominant to the weaker alleles, but either is capable of completing the expression of the other. (3) *Reciprocal differences are due to dominance, and not, as in other*

known cases, to homozygosity of one parent. Other genes at different loci are believed to be able to exert modifying effects, especially when associated with the recessive S alleles.

It would be very desirable to have these findings checked by experiments with *C. foetida* subsp. *commutata*; and to have these results compared with the basis of self-incompatibility in other species of *Crepis*. The general role of self-incompatibility in the evolution of various *Crepis* species should eventually be worked out.

CYTOGENETIC PROBLEMS

Among the many cytogenetic problems which remain to be solved in *Crepis*, only a few can be mentioned here. These are problems which have been recognized by the author and his associates but which it has not been possible to attack.

Chromosome pairing in interspecific hybrids.—As was pointed out on page 58, it is desirable that there be a well-planned repetition, on a much larger scale, of Avery's (1930) cytological studies on chromosome pairing in interspecific hybrids having *Crepis leontodontoides* as one parent. The general significance of these and similar experiments in hybridizing species of *Crepis* has been shown (Babcock and Emsweller, 1936, p. 359) to support the conception that all species of *Crepis* had a common origin and are still more or less similar in genetic composition. But it was also pointed out (*op. cit.*, p. 355) that, in order to generalize concerning the phyletic relations of the species on the basis of comparative meiotic regularity, there should be several series of hybrids in each of which a single species is used as one parent of each cross. The above suggestion, that *C. leontodontoides* might be used as the common parent in one such series, is based on Miss Avery's success in crossing it with several widely separated species and more recent crosses between it and still other species. From its phylogenetic relations it seems probable that *C. Bungei* might be used successfully in another such series of hybridizations. Obviously, such investigations as these can be carried on only where a large collection of *Crepis* species, representing as many sections as possible, is maintained for research purposes.

Structural hybrids and speciation.—The bearing of structural hybrids on speciation in *Crepis* provides an alluring field for further research. The demonstrations by Tobgy (1943) and Sherman (1946) of the mechanism by means of which reductions in chromosome number have been accomplished in *Crepis* are of fundamental importance. Additional evidence, however, is desirable and a number of similar investigations are possible, provided that the necessary artificial hybrids can be produced. Two such studies which appear to be unusually promising are those which concern the phyletic relations between each of the two other 3-paired species, *C. capillaris* and *C. Zacintha*, and its closest 4-paired relatives. In *C. capillaris* only one very close 4-paired species exists, namely, *C. parviflora*, whereas the experiments with *C. Zacintha* should include not only *C. multiflora* and *C. Dioscoridis* but also *C. patula* (cf. Part II, pp. 742, 743).

Location of heterochromatin in Crepis chromosomes.—Heterochromatin distribution in the chromosomes of *Crepis* species, and its bearing on chromosome morphology and on changes in chromosome number through reciprocal translocations, is another almost untouched field of research. Sufficient evidence was discovered by Tobgy (1943, pp. 72–73) to show that this is indeed a very promising field.

Specific chromosome size.—The factors controlling chromosome size is another problem, the importance of which was recognized by Tobgy (*op. cit.*). In his doctor's dissertation (filed in the University of California Library) he has the following to say (pp. 129–130, 131).

If it is true that the difference in thickness between the *C. fuliginosa* and *C. neglecta* chromosomes is due to their differential synthesis of matrical chromatin, then the fact that this difference is still maintained in the parental chromosomes in the F₁ hybrid and in the second generation plants indicates that such differential activity is also autonomously controlled within the chromosomes themselves rather than by the whole genotype. The interesting observation that, in the second generation, the new chromosomes have either the *fuliginosa* or the *neglecta* thickness throughout their length, even though they had a distal segment of one arm from a parental origin different from that of the remainder of the chromosome body, suggests that the amount of the matrical chromatin in these distal segments is controlled by the centromeres or the procentric segments, either directly or through a kind of position effect (cf. Muller, 1939). The main point is, however, that chromosome thickness here is not controlled by the whole genotype but within each chromosome individually.

For the present, it must be concluded that there is nothing in the nature of a general rule with respect to disappearance or maintenance of size differences between parental chromosomes in interspecific hybrids; the outcome in a given hybrid would depend on what factors are responsible for the initial size differences in the chromosomes of the two parent species, and on whether these factors are controlled by the whole genotype or within the individual chromosomes themselves.

Tobgy's findings, then, make it obvious that much further research must be made in order to throw light on the nature of size differences between the chromosomes of related species. With the marked differences known to exist in various species of *Crepis*, this genus seems to offer especially favorable material for further research in this field.

In conclusion, the author regretfully acknowledges that "the gene contents of not a single species of *Crepis* is anywhere nearly as well explored as that of *Drosophila melanogaster*, *Zea mays*, or *Gossypium*" (Mayr, 1943), although the original purpose in attacking *Crepis* was to subject at least one species to intensive genetic analysis. Practical considerations contingent upon very limited funds for assistance, however, soon made it necessary to choose between concentration of effort upon the analysis of a single species or upon research on interspecific hybrids, which, it must be said, began, early in the history of the investigations, to offer alluring possibilities. Because of the technical difficulties involved in hybridizing and selfing, this genus can never compare with any of those mentioned above, nor with *Antirrhinum* and *Nicotiana*, in suitability for intensive genetic analysis. But these difficulties need not prevent further cytogenetic research on species and hybrids such as has been suggested above.

The other criticism of Mayr (*loc. cit.*), that "as far as taxonomy is concerned, the degree of perfection which intraspecific population analysis has reached in fishes, mammals and birds does not seem to be approached in *Crepis*," was not based on the present monograph. Nevertheless, it probably holds true in large measure. As Mayr points out, "filling this gap will require the statistical analysis of future mass collections." The need for such research is especially pronounced in analyzing such a difficult complex as *Crepis vesicaria*, *C. foetida*, *C. albida*, or *C. Dioscoridis*. The statistical analysis of mass collections (in the sense of Anderson, 1941) should throw much needed light on such difficult problems, especially when these studies are supplemented by cytological observations and genetic tests of all questionable forms. Undoubtedly, a more refined and thorough population analysis offers an attractive opportunity for the modern taxonomist to place our knowledge of *Crepis* on a sounder basis.

APPENDIX 2

THE BEARING OF THE EVOLUTION OF *CREPIS* ON THE ORIGIN OF THE ANCESTORS OF EURASIATIC CROP PLANTS

THE CONCLUSION that *Crepis* had its origin and early development in northern Central Asia deserves consideration in attempting to establish the actual region of origin of the progenitors of the principal Eurastic crop plants. The demonstration by Vavilov (1927, 1928) that cultivated plants have five principal geographic gene centers seems to have resulted generally in the assumption that these crop plants had their complete evolution from earliest beginnings in those same centers. That such an assumption is untenable is obvious from the fact that three of these five regions (southwestern Asia, the Mediterranean region, and the highlands of Mexico, Guatemala, Colombia, and Peru) were completely submerged by the great marine transgression which occurred about the middle of the Cretaceous period (cf. Seward, 1941, fig. 106). Of the other two regions, Abyssinia was a part of Gondwana Land, and the southern part of southeastern Asia was submerged in Cretaceous times, although most of China was part of Angara Land during this period.

Abyssinia has been recognized by Vavilov as an important gene center, and it may be significant that it was part of Gondwana Land since before the Carboniferous period (Seward, 1941, fig. 49). But southwestern Asia and the Mediterranean regions were also important, and these regions were not only submerged during the Cretaceous period, when the flowering plants were strongly developing, but again in Middle Oligocene they were almost completely covered by Tethys and its connections to the northeast and southeast. Hence, the *ancestors* of the many crop plants which developed in these two regions must have had their origin and early development elsewhere.

The history of *Crepis* suggests that the ancestors of the crop plants which were developed by early man in southwestern Asia and the Mediterranean region may have migrated into those regions during Tertiary times from the Angara region. But these crop plants represent various families, and they undoubtedly have diverse histories. Some may have come from the south, for it is known that elements of the Gondwana flora migrated as far north as southern Central Asia (cf. Korovin, 1935). The possibility, however, that many of these *progenitors* of our cultivated plants were derived from the original Angara flora seems worth considering. In Cretaceous times Angara included most of China and that part of Siberia as far west as the Altai region.

The conclusion of Vavilov (1931b, p. 44; and see Huxley, 1940, p. 550) that Central Asia "cannot be regarded as the primary base of species formation," with reference to our crop plants, is based on the paucity of forms of cultivated plants in that region and on the apparent absence of well-known wild relatives along the route of the one expedition which he made. It seems fair to question whether more extensive explorations might not reveal the presence of some of those wild relatives or, if not, whether other less closely related species, representing possible ancestors of present-day crop plants, may not exist in the Altai-Tien Shan region.

But, even if northern Central Asia was not a region of origin for the ancestors of some of our crop plants, there still remains the vast region farther to the east,

where important discoveries of early angiospermous plants have recently been made (Kryshtofovitch, 1933). It seems very probable that the important crop plants of southeastern Asia had their actual origin (ancestral forms) farther north in Asia. It may be that from that same center in northeastern Asia came the progenitors of some at least of the important crop plants which were developed by early man in southeastern, southern Central, and southwestern Asia as well as in the Mediterranean region.

It is even possible that in that same Angara center there evolved the original ancestors of *Zea mays*, which has long been considered of New World origin. The recent discovery by Anderson (1943) that a certain South American variety of maize resembles certain Oriental varieties reopens the entire question of Oriental versus Occidental origin of this species.

APPENDIX 3

THE BEARING OF THE DISTRIBUTIONAL HISTORY OF CREPIS ON THE REGION OF ORIGIN OF SOME ANGIOSPERMS

IN HIS RECENT important book, *Foundations of Plant Geography*, published after the present monograph was completed, Cain (1944) emphasizes the historical aspects which are essential for an adequate understanding of present-day plant distribution. But, in the opinion of the present author, he sometimes fails to give due consideration to all the historical possibilities which should be recognized in attempting to explain such problems. For example, in his discussion of discontinuous distributions (p. 247), he refers to *Menodora* (cf. Steyermark, 1932), which is restricted to southwestern United States and Mexico, southern South America, and South Africa. According to Cain: "Steyermark finds the center of variation of the genus to be in Mexico and concludes that it had a more continuous geographical continuity at least before the end of the Cretaceous period. He believes the most logical explanation to result from the postulation of a land bridge across the south Atlantic which was obliterated by the Upper Cretaceous."

Apparently, neither Steyermark nor Cain considered the possibility of a far northern origin of the genus, followed by holarctic distribution and eventual migration into South America and Africa. The fact that *Menodora* is characteristically a xerophytic group does not lessen the probability of this hypothesis. On the contrary, the probability is actually increased, since the present geographic subgroups within the genus may logically be considered as relics of an earlier, wide distribution. It is only necessary to assume that the genus has been able to persist at all through the evolution of adaptation to xeric conditions. The same reasoning would apply to the other xerophytic genera with similar distributions which are mentioned by Cain, namely, *Hoffmanseggia*, *Fagonia*, and *Thamnosma*. This is especially clear in *Thamnosma*, in which the present-day distribution more nearly resembles that of *Crepis*, because *Thamnosma* belongs in the same subfamily of the Rutaceae as the genus *Citrus* and its close relatives, which are indigenous in eastern Asia and exist under mesophytic conditions.

The basic problem involved in explaining the widely disrupted distributions of these xerophytic groups is essentially the same as that considered by Fernald (1931) in his illuminating discussion of several other groups of plants which are now restricted to certain regions in North and South America, southern or tropical Africa, and southeastern Asia, Malaysia, or Australia. Fernald (*op. cit.*, p. 61) recognized two alternative hypotheses: Either these disrupted distributions were derived from "the widespread boreal flora of the Cretaceous and early Tertiary," or they "spread across a hypothetical trans-Atlantic land"; and he states that the former "seems to me the logical deduction." The present distribution of *Crepis*, which extends into northern Mexico, South Africa, and southeastern Asia, presents a generally similar distributional picture; and the northern Asiatic origin of this genus is clearly indicated.

APPENDIX 4

OVARY ANATOMY AS A PHYLOGENETIC CRITERION IN CREPIS

IN HIS STUDY of *Dubyaea*, the primitive endemic genus from which *Crepis* and other genera of the Crepidinae are believed to have descended, Stebbins (1940) found that the species of *Dubyaea* and of another relic, the Sino-Himalayan genus *Soroseris*, possess supernumerary vascular strands in the young ovary. He also reported that some of the most primitive species of *Crepis* have supernumerary strands of vascular tissue, whereas some of the more advanced species have the reduced vascular system of the ovary which is found most frequently in the Cichorieae. At that time it was not feasible for the present author to make a more extensive study of ovary anatomy in *Crepis*; but more recently it has been possible to examine a number of species. These species have been selected so as to represent the most primitive and most advanced types in the genus. Furthermore, in order to determine whether there is correlation between relative phylogenetic position within the sections and presence or absence of supernumerary vascular strands, most of the species in the first nine sections were included. Using the method of bleaching reported by Stebbins (1938), it was found practicable to examine the ovaries in temporary mounts after hardening in alcohol. But in a few species having a dense ovary wall it was necessary to give a second or third exposure to hydrogen peroxide; and even then the results were not always satisfactory. This was especially notable in *C. terglouensis* and *C. alpestris*. The species examined are listed below by sections; the order within each section, indicated by Arabic numerals, is the phylogenetic order already determined on the basis of morphology and cytogenetics. Following the name of each species is given the number, in parentheses, of the herbarium sheet of the University of California specimen used or the culture number of the few dried vouchers from greenhouse or garden cultures used. Lastly, is given the minimum and maximum number of supernumerary ovular vascular strands counted in the several (mostly 5-7) ovaries examined.

- Section I. 1. *C. sibirica* (28.1997-5) 2-5
 2. *C. geracioides* (565334) 3-6
 3. *C. viscidula* (489404, 489393) 3-6
 4. *C. paludosa* (74022) 0-1
 4. *C. paludosa* m.v. no. 1 (442874) 1-4
- Section II. 1. *C. kashmirica* (446402) 2-5
- Section III. 1. *C. pygmaea typica* (656651) 2-4
 1. *C. pygmaea anachoretica* (639610) 4-6
- Section IV. 1. *C. terglouensis* (463914) 0-2 (ovary wall dense)
 2. *C. rhaetica* (669413) 4-5
 3. *C. Jacquini* (463918) 1-3, mostly 2
 4. *C. aurea typica* (669458) 0-1
 4. *C. aurea lucida* (429387) 1-2
 5. *C. chrysantha* (598101) 2-3
 8. *C. albiflora* (565326) 0
- Section V. 1. *C. lapsanoides* (194338) 5-7
 8. *C. Mungierii* (429360) 0-2
- Section VI. 1. *C. pontana* (669402) 4-7
 2. *C. conyzaeifolia* (429374) 3-5
 3. *C. blattarioides* (406905) 2-4
- Section VII. 1. *C. albida asturica* (31.2957-7) 2

- Section VIII. 1. *C. kilimandscharica* (494389) 4-5
 3. *C. alpestris* (669456) 0-3 (ovary wall dense)
 17. *C. scaposa taraxaciiformis* (565329) 4
 26. *C. Bruceae* (557860) 0
- Section IX. 1. *C. tingitana* (1574) 2-3
 2. *C. leontodontoides* (259899, 669381) 0
 3. *C. suberosistris* (429511) 0
- Section XX. 1. *C. alpina* (463886) 0
 3. *C. rubra* (2417, 2744) 0
- Section XXIV. 1. *C. nicaeënsis* (31.2958-1) 0
 2. *C. capillaris* (29.2176-5) 0
- Section XXVII. 3. *C. belluidifolia* (33.2940-7) 0
 7. *C. senecioides* (30.1044-1-2-8) 0

These data make it clear that the primitive sections (I-VIII) are characterized by the presence of supernumerary vascular strands in the ovary, and that the advanced sections (XX, XXIV, XXVII) all have the reduced type of vascular system. In the intermediate or bridging group, section IX, the most primitive member has supernumeraries, whereas the other two have none. Further, in sections I, IV, V, VI, and VIII, the one least primitive species examined in each section either has a greatly reduced number of strands or lacks supernumeraries entirely, as in *C. albiflora* of section IV and *C. Bruceae* of section VIII.

Some irregularities, for example the differences in number of supernumerary strands recorded for *C. sibirica* and *C. geracioides* or for *C. Jacquini* and *C. chrysanthia*, exist within the primitive sections I, IV, and VIII, but do not obscure the general picture. The marked difference between *C. terglouensis* and *C. rhaetica* or between *C. alpestris* and *C. scaposa* may be due to obscuration of some supernumeraries by the dense wall in two of these species. The apparently lower number in *C. aurea* as compared with *C. chrysanthia* may be an actual difference, since the former is definitely more reduced in size of the plant and its parts.

Thus, it may be concluded that a higher number of vascular strands in the ovary is positively correlated with degree of primitiveness as determined from external morphology. Furthermore, the high numbers of supernumerary strands present in the most primitive species (I-1, 2, 3; II; III; IV-2; V-1; VI-1; VIII-1) is additional evidence supporting the assumption of close relationship between *Crepis* and its putative ancestral genus, *Dubyaea*.

PLATE

PLATE 1

Fossil and present-day achenes of *Crepis*. The fossil specimens are designated by a, b, c; the others, by a', b', c'.

a, a', *Crepis tergluensis* (Hacq.) A. Kern.

a, from Reid and Reid (1916, pl. 17, no. 30).

a', from a collection of seeds received from the Botanic Garden, Innsbruck, Austria, in 1935.

b, b', *Crepis conyzaeifolia* (Gouan) Dalla Torre.

b, from Reid and Reid (1916, pl. 17, nos. 26, 27).

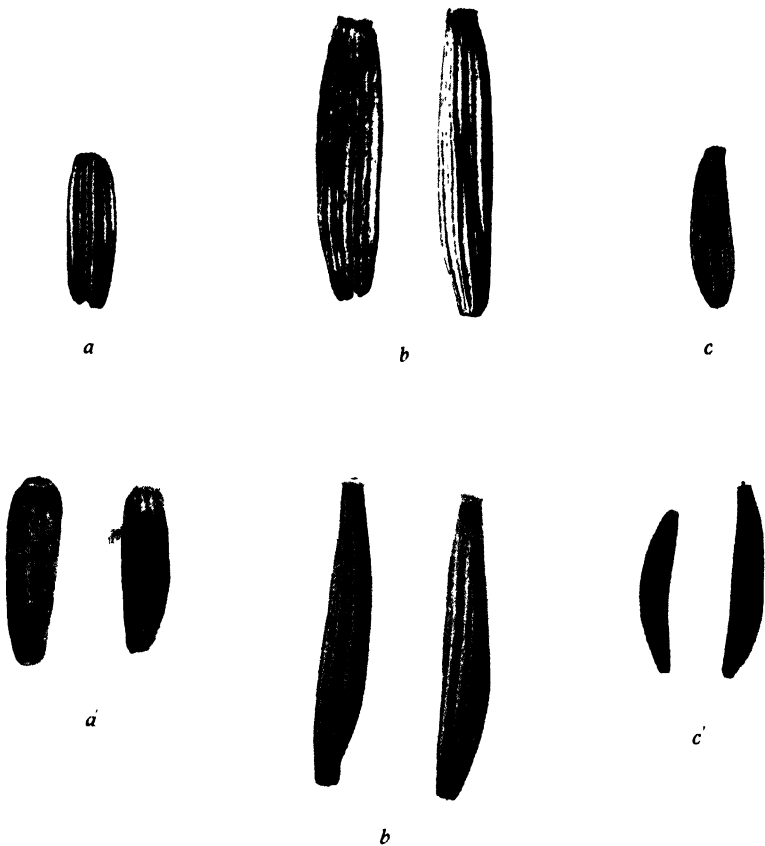
b', from Stefanoff in 1929 (UC 470082).

c, c', *Crepis mollis* (Jacq.) Asch.

c, from Reid and Reid (1908, pl. 13, no. 96).

c', left, from Herb. Willd. (B) n. 14680-1.

right, from hort. genet. Calif. 28.2201-12 (UC 531725).



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**LEE BONAR
A. S. FOSTER
H. L. MASON**



THE GENUS CREPIS

PART TWO

Systematic Treatment

BY

ERNEST BROWN BABCOCK

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Part Two

SYSTEMATIC TREATMENT

Part One of this work (University of California Publications in Botany, Volume 21) subtitled

The Taxonomy, Phylogeny, Distribution, and Evolution of Crepis

embraces pages i-xii + 1-198, in which are included frontispiece, plate 1, text figures 1 to 11 and A to D, and tables 1 to 12. Additional to the eight chapters of Part One are appendixes 1 to 4, references (bibliography), and index.

Part Two embraces pages i-x + 199-1030, in which are included plates 2 to 36, text figures 12 to 305, and tables 13 to 19.

SYSTEMATIC TREATMENT OF THE GENUS CREPIS

GENERAL PLAN

FOLLOWING the history and diagnosis of the genus, the diagnoses of the sections, and the key to the sections, the sections of genus *Crepis* are taken up in numerical order. Each section, except the 3 monotypic ones, is introduced with a discussion of the relationships of the species in the section and of their geographic distribution, which, except in sec. 15, the American allopolyploid species, is illustrated by a map. Then follows a key to the species in the section. Only the 2 largest sections, 8 and 10, are divided into subsections, but in these, also, each has one key which suffices for all the species in the section. The numerical order of the sections and of the species in each section or subsection roughly indicates their phylogenetic position in the genus. Phylogenetic relations, however, cannot be adequately represented by a linear arrangement; and this fact will be evident to anyone who compares the most advanced species of one section with the most primitive species in the next. A chart, fig. 4 of Part I, attempts to depict the phyletic relations between all of the sections.

DESCRIPTIONS

Latin diagnoses.—Latin diagnoses are provided for all new sections, species, and subspecies which are published here for the first time.

Species descriptions.—Although consistency in description of the species, particularly where it concerns the description of parts and their sequence, has been aimed for, in species comprising 2 or more subspecies the general description of the species is usually more or less abbreviated by omitting those parts in which the subspecies differ, they being left to be presented in the descriptions of the subspecies. In such species the general description is followed by a key to the subspecies. The descriptions of subspecies will be found consistent within each species but not always between different species.

Illustrations.—Each species is illustrated by a figure, including, as a rule, a drawing to show the general habit of the plant. When it has been impossible to include such drawing, plates showing one or more herbarium specimens are provided. The drawings of plant parts in the figures are directly comparable. The actual magnifications, all of which are stated in the accompanying legends, are, as a general rule, as follows: flower heads $\times 2$; involueral bracts and florets $\times 4$; anther tubes, achenes, and pappus setae $\times 8$; and details of the anther appendages $\times 32$. Being so given, a rapid comparison of one species with another will be possible. For most of the species which have been examined cytologically, an illustration of the chromosomes, based on the publications of Babcock and Cameron or Babcock and Jenkins, is included in the figure. (See list of references given below.)

Measurements.—All of the measurements of plants and their parts are made in metric units. Elevations are indicated in meters, and distances in kilometers. So far as possible, the dimensions of plant parts given in the descriptions represent averages from several specimens, or else they are the observed range of size. But in a good many species where material is very scanty, the sizes given in the description may represent only a single specimen. All measurements are based on herbarium specimens, but, as a rule, the measurements of florets and their parts are from boiled material. Most of the drawings of floret, anther tube, and appendages were copied by the artist from original drawings made by the author.

Geographic distribution and ecologic relations.—In defining the geographic distribution of a species, the information obtained from the observation of the her-

barium specimen has been supplemented by comparison with other floras and by consulting pertinent literature. In many species, however, definite information is lacking on the exact limits of the range. In indicating the distribution of such a species on a map, a wavy line is used in that part of its range where the exact boundary is unknown. The species are extremely variable in the amount of information available concerning their ecologic relations. For many of them no such data exist except those gained indirectly by deduction from the location of the station or stations where the specimens were collected. Effort has been made to bring together all the available evidence from such authors as Hegi, Pax, Braun-Blanquet, Rübel, and Willkomm, and to supplement this by the observations of many collectors, including the present author.

Citation of type and critical specimens.—Whenever possible the type of the species has been examined, together with specimens critically affecting synonymy. When this has been done the location of the type and such specimens is usually indicated in a paragraph following the geographic distribution. In some, however, the type is merely given in the citation of specimens. Even though Linnaeus did not base his species on types, yet the specimens which he determined were considered as typical (cf. Svenson, H. K., *Rhodora* 47 [562]: 273–302; [563]: 363–388. 1945). In certain Linnaean species, however, it was necessary for the present author to use his own judgment as to which of two or more specimens should be accepted as the type. For example, in the Linnaean herbarium in London there are two specimens labeled *paludosum* (*Hieracium paludosum* L.). One of these is typical of *Crepis paludosa* (L.) Moench as that species is generally recognized; the other is evidently *Crepis lapsanoides* (Gouan) Tausch. There is no question as to which should be accepted as the Linnaean “type.”

Variability.—Species known at present to be monomorphic are so indicated just preceding the citation of specimens. Absence of such notation means that the species is sufficiently variable to be classed as polymorphic, even though subspecies may not be recognized. In many species a discussion of the nature of the variability is given at this point.

Citation of specimens.—The main purposes of the citation of specimens are to illustrate the variations existing in the species and to indicate, so far as possible, the geographic distribution. The name of the collector and the number of the specimen, if available, are always italicized; and the abbreviations indicating the herbaria containing the specimens follow, in parentheses, the citation. An index to the collectors of the specimens cited is provided at the end of this work, on pages 999–1016.

Minor variants.—In all of the polymorphic species there are forms which deviate more or less from the type. Moreover, because certain of these forms are more “typical” of the species than the type, some of the variants in each species have been described by earlier taxonomists in the category of *forma*, *varietas*, *subspecies*, or *species*. When it has appeared to the present author that such variants, whether or not they have been published with Latin names, are likely to give trouble to future workers in the identification of specimens, they have been given numbers and listed under the heading “minor variants.” Each one is described, at least to some extent, and specimens are cited. When Latin names have been given them in the past, these appear as synonyms in parentheses immediately following the number of the variant. When a species consists of 2 or more subspecies, the minor variants in each subspecies follow the citation of specimens of that subspecies, regardless of numerical order, since the numbers were applied to them in the order in which they happened to come to the author’s attention.

Synoptical comparisons.—In certain pairs or groups of species or subspecies, the delimitation of which is critical or difficult, comparable data are presented in tabular form near the end of the description of one of the species. These tables will presumably be helpful to those interested in the problems involved.

ABBREVIATIONS AND CITATIONS

MISCELLANEOUS ABBREVIATIONS

The following abbreviations have been used in the taxonomic descriptions, in the citation of specimens, and in the text.

acc., according	mm, millimeter
alt., altitude	±, more or less
apm., forma apomictica	Mt., Mount or Mountain
Arch., Archipelago	Mts., Mountains
cm, centimeter	μ, micron(s)
Co., County	m.v., minor variant or variants
Cr., Creek	N., north, northern
cult., cultures, cultivation	N.E., northeast, northeastern
dis., dissected and opened out flat	N.W., northwest, northwestern
dist., district	Pen., Peninsula
dm, decimeter	p.p., pro parte, in part
E., east, eastern	Prov., Province
ex, from	q.v., which see
<i>fide</i> , according to, on the word of	R., River
I., Island	reg., region
Is., Islands	S., south, southern
in herb., in a private or unspecified herbarium	S.E., southeast, southeastern
in Herb., in the Herbarium of (followed by the name of an institution or governmental unit)	sen. lat., sensu lato, in the wider sense
in sic., in dried specimens	sen. str., sensu stricto, in the narrower sense
km, kilometer	S.W., southwest, southwestern
leg., collected by	spec., specimen(s)
loc. class., the type locality	spec. unic., specimen unicum, a single specimen
m, meter	Terr., Territory
	W., west, western

ABBREVIATIONS FOR HERBARIA CITED

Alger	Algiers, Herbarium, Institute de Botanique, Université d'Alger, Algeria.
Amani	Amani, Herbarium, East African Agricultural Research Station, Amani, Tanganyika.
B	Berlin, Herbarium, Botanischer Garten und Museum, Berlin-Dahlem, Germany.
Bar	Barcelona, Herbario de museo de ciencias naturales de Barcelona, Spain.
BB	Barbey-Boissier (included in the Boissier Herbarium, see Bo).
Blake	Blake, Private Herbarium of Dr. S. F. Blake, 2817 First Road, N, Arlington, Virginia.
BM	British Museum, Herbarium, British Museum (Natural History), Cromwell Road, London, S.W. 7.
BML	British Museum—Lacaita, Lacaita Herbarium, British Museum (Natural History), Cromwell Road, London.
Bo	Boissier, Herbarium Boissier, Université de Genève, Switzerland.
Bornm	Bornmüller, Private Herbarium of Dr. J. Bornmüller, Amaliseestrase, 27, Weimar, Germany.
Br	Brooklyn, Herbarium, Brooklyn Botanic Garden, Brooklyn, New York.
Brussel	Bruxelles, Herbarium, Jardin Botanique de l'Etat, Bruxelles, Belgium.
Budapest	Budapest, Herbarium, National Hungarian Museum, Budapest.
Bur	Burnat (included in the De Lessert Herbarium, see DL).
Bur-S	Burnat Supplement (<i>ibid.</i>).
BW	Berlin, Willdenow Herbarium, in Botanischer Garten und Museum, Berlin-Dahlem, Germany.

- C Copenhagen, Herbarium, Hortus Botanicus Haviensis, Copenhagen.
- CA California Academy, Herbarium, California Academy of Sciences, San Francisco, California.
- Calcutta Calcutta, Herbarium, Calcutta Botanic Garden, Calcutta.
- Clo Clokey, Private Herbarium of Dr. Ira W. Clokey, South Pasadena, California.
- CM Copenhagen Museum, Herbarium, Universitetets botaniske Museum, Copenhagen.
- Co Cornell, Herbarium, Cornell University, Ithaca, New York.
- CU Catholic University, Herbarium of the Catholic University of America, Washington, D. C.
- CP College of Pharmacy, Herbarium, New York College of Pharmacy of Columbia University, New York City.
- DC De Candolle, De Candolle Herbarium, Conservatoire et Jardin Botaniques, Geneva.
- DD Dehra Dun, Herbarium, Forest Research Institute, Dehra Dun, India.
- DL De Lessert, Herbarium Generale, De Lessert Herbarium, Conservatoire et Jardin Botaniques, Geneva.
- DS Dudley Stanford, Dudley Herbarium, Stanford University, California.
- DW Delaware Wilmington, Herbarium, Delaware Natural History Society, Wilmington, Delaware.
- E Edinburgh, Herbarium, Royal Botanic Garden, Edinburgh 4.
- FI Florence, Herbarium, Istituto Botanico de Universite di Firenze, Italy.
- FM Field Museum, Herbarium of The Field Museum, Chicago.
- Genoa Genoa, Herbarium, Istituto Botanico, University of Genova, Genova, Italy.
- G Gray Herbarium, Harvard University, Cambridge, Massachusetts.
- Grenoble Grenoble, Herbarium de l'Université de Grenoble, France.
- Hayek Hayek, Private Herbarium of Dr. Augustus Hayek, Margaretenstrasse 82, Wien V, Austria.
- IIU Hebrew University, Herbarium, Hebrew University, Jerusalem, Palestine.
- K Kew, Herbarium, Royal Botanic Gardens, Kew, England.
- L Linnaeus, Linnaean Herbarium, Linnaean Society, Burlington House, London.
- Len Leningrad, Herbarium, Jardin Botanique Principal, Leningrad, U. S. S. R.
- Lund Lund, Herbarium, Botaniska Museet, Lund, Sweden.
- Minn Minnesota, Herbarium, University of Minnesota, St. Paul, Minnesota.
- Mo Missouri, Herbarium of the Missouri Botanical Garden, St. Louis, Missouri.
- Mosc Moscow, Herbarium, University of Moscow, Moscow, U. S. S. R.
- Moss Moss, Private Herbarium, Professor C. E. Moss, University of Witwatersrand, Transvaal.
- Ms Montpellier, Herbarium, Institute de Botanique, Montpellier, France.
- Mu Munich, Herbarium, Botanischer Museum, München, Germany
- MW Museum Vienna, Herbarium, Naturhistorische Museum, Wien, Austria.
- Naples Naples, Herbarium, Istituto Botanico, Naples, Italy.
- ND Notre Dame, Herbarium, Notre Dame University, Notre Dame, Indiana.
- NY New York, Herbarium, New York Botanical Garden, New York City.
- Nev Nevada, Herbarium, Nevada Agricultural Experiment Station, Reno, Nevada.
- Or Oregon, Herbarium, University of Oregon, Eugene, Oregon.
- Oxford Oxford, Herbarium, Botanical Society and Exchange Club of the British Isles, Oxford, England.
- Oxford-D Oxford, Druce, Private Herbarium of G. C. Druce, Oxford, England.
- P Paris, Herbarium, Museum d'Histoire Naturelle, Paris.
- PA Philadelphia Academy of Sciences, Herbarium, Philadelphia.
- Pal Palestine, Herbarium Palaestinum, Hebrew University, Jerusalem, Palestine.
- PC Paris, Cosson herbarium, Museum d'Histoire Naturelle, Paris.
- PD Prague Deutsch, Herbarium, Botanischer Institut, Deutscher Universität, Praha II, Czechoslovakia.
- PM Prague Museum, Herbarium, National Museum of Czechoslovakia, Praha, Czechoslovakia.
- Po Pomona, Herbarium of Pomona College, Claremont, California.
- Pre Pretoria, National Herbarium, Pretoria, South Africa.
- PVel Prague Velenovsky, Velenovsky Herbarium, Czechoslovak University, Praha, Czechoslovakia.
- RB Reuter-Boissier (included in the Boissier Herbarium, see Bo).
- RM Rocky Mountain Herbarium, University of Wyoming, Laramie, Wyoming.
- Rome Rome, Herbarium, Regio Istituto Botanico, Rome.
- Sofia Sofia, Herbarium de l'Université de Sofia, Bulgaria.

Sofia-M	Sofia Museum, Herbarium, Museum d'Histoire Naturelle, Sofia, Bulgaria.
Stockholm	Stockholm, Naturhistoriska Riksmuseet, Botaniska Avdelningen, Stockholm 50.
Torino	Turin, Herbarium, Istituto Botanico de Universite de Torino, Turin, Italy.
UC	University of California, Herbarium, Berkeley, California.
UCf	<i>Ibid.</i> , fragments of critical specimens from other herbaria.
Uppsala	Uppsala, Herbarium, Botaniska Institutionen, Uppsala, Sweden.
US	United States, United States National Herbarium, Washington, D. C.
UWG	University of Vienna-General, Herbarium, Botanischer Garten und Institut, Wien, Austria.
UWH	University of Vienna-Halacsy, Halacsy Herbarium, Botanischer Garten und Institut, Wien, Austria.
UWK	University of Vienna-Keck, Keck Herbarium, Botanischer Garten und Institut, Wien, Austria.
UZ	University Zurich, Herbarium, Botanischer Museum, Universität, Zurich, Switzerland.
Wellesley	Wellesley, Herbarium, Department of Botany, Wellesley College, Wellesley, Massachusetts.
Will	Willamette, Herbarium, Willamette University, Salem, Oregon.
Wis	Wisconsin, Herbarium, University of Wisconsin, Madison, Wisconsin.
Wn	Washington, Herbarium, University of Washington, Seattle, Washington.
WSC	Washington State College, Herbarium, State College of Washington, Pullman, Washington.
Ya	Yale, Herbarium of the Osborn Botanical Laboratory, Yale University, New Haven, Connecticut.

ABBREVIATIONS FOR WORKS OFTEN CITED IN THE TEXT

In the discussions of distribution, ecology, and relationships of species, the following works are referred to by the abbreviations indicated. As a rule pagination is stated in parentheses following the abbreviation. Nomenclatural citations are abbreviated in the conventional manner, not by the style indicated here.

- Adamovic = Adamovic, L. Die Vegetationsverhältnisse der Balkanländern (Mösische Länder) umfassend Serbien, Altserbien, Bulgarien, Ostrumelien, Nordthrakien und Nordmazedonien. [Engler, A., u. Drude, O. Die Vegetation der Erde. XI.] Leipzig. 567 pp. 1909.
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HISTORY, DIAGNOSIS, AND DESCRIPTION OF THE GENUS

HISTORY

The nomenclatural history of *Crepis*, like that of many other natural groups, has been one of vacillation between "splitting" and "lumping" according to the peculiar tendencies exhibited by various synantherologists. In the first edition of *Species Plantarum*, under *Crepis*, Linnaeus included 13 species, 10 of which are still accepted in *Crepis* and which represent secs. 1, 3, 10, 19, 20, 24, 25, and 27 of the present author. This certainly indicates a conservative attitude and a tendency toward an inclusive treatment. At the same time it may be noted that Linnaeus

also published 9 species of *Crepis*, mostly in the first edition of *Species Plantarum*, under 4 other genera: 6 under *Hieracium*, and 1 each under *Leontodon*, *Hypochaeris*, and *Lapsana*. This early confusion of *Crepis* with other genera of the Cichorieae has persisted into the present century.

In 1794 Moench (Meth. 534–537) recognized 3 genera, *Crepis*, *Catonia*, and *Barkhausia*, which were merged into one a century later by Bentham and by Hoffmann. But in the meantime there were several swings of the pendulum between the extremes of splitting and fairly conservative lumping.

Cassini, who was the first to attempt a general revision of the Compositae, published important contributions to the subject during the first third of the nineteenth century. But his proclivity toward the useless multiplication of generic names, exemplified by his treatment of some of the species now accepted in *Crepis*, caused him to distribute them among at least 14 genera, as follows: *Anisoderis*, *Barkhausia*, *Brachyderca*, *Catonia*, *Crepis*, *Gatyona*, *Hostia*, *Intybellia*, *Nemauchenes*, *Omalocline*, *Paleya*, *Phaeccasium*, *Pterotheca*, and *Zacintha*. The last 8 names in this list appear as section names in the present monograph. Although this plethora of genera was a cause of confusion in later years, yet one result of Cassini's careful observations was to make clear the distinction between *Crepis* and other large related genera, such as *Hieracium* and *Lactuca*.

Monnier, in his often-cited work (*Essai Hierac.* 1829), recognized 2 genera of Cassini (*Omalocline* and *Intybellia*) and erected 2 new genera, *Aracium* and *Soyeria*. The former was especially unfortunate, since it included only *Crepis paludosa* (L.) Moench and *Mulgedium alpinus* Less., neither of which, as was pointed out by Bischoff (258), fits the genus description. Under *Soyeria*, which has become sec. 6 in this monograph, were included 4 species of *Crepis*.

Somewhat more conservative is the treatment of Lessing (*Syn. Gen. Comp.* 1832), who merged 5 of Cassini's genera under *Crepis* and 4 under *Barkhausia*. At the same time he recognized *Pterotheca*, *Intybellia*, *Gatyona*, and *Nemauchenes* of Cassini as genera, along with *Lagoseris* M. B., *Aracium* Neck., *Soyeria* Monn., and *Zacintha* Gaertn. It is to his credit, however, that he placed *Zacintha* near *Nemauchenes* and *Gatyona*, thus showing, unlike Hoffmann (see below), who placed it in another subtribe of the Cichorieae, that he recognized its true relationships. It should be noted that Lessing included under *Crepis* the genus *Aetheorrhiza* Cass., a genus which is excluded from *Crepis* by the present author (cf. Babcock and Stebbins, *Univ. Calif. Publ. Bot.* 18: 227–240. 1943).

De Candolle, in the *Prodromus* (vol. 7, 1838), followed Lessing's general treatment of this group of species. He recognized *Barkhausia* as a genus including 45 species, more than half of which are synonyms. Under *Crepis* he included 56 species, many of which are synonyms, and 19 others as doubtful ones, most of which are synonyms. Of Cassini's genera, de Candolle included in the *Prodromus*, *Phaeccasium*, *Brachyderca*, *Crepis* (as sec. *Eucrepis*), and *Catonia*. In addition to *Barkhausia* and *Crepis*, de Candolle recognized *Zacintha*, *Endoptera* (including *Gatyona* and *Nemauchenes*), and *Pterotheca* as genera. He differed from Lessing in separating *Aetheorrhiza* as a genus. Thus, de Candolle must be credited with adopting a fairly conservative attitude concerning number of genera recognized. On the whole, however, his treatment of this group, both with respect to genera recognized and the systematic treatment of *Barkhausia* and *Crepis*, is very unsatisfactory from a present-day standpoint.

In 1851 Bischoff (244–329) issued a detailed report of a study of 28 species of *Crepis* occurring in central and S. Europe. Within this group he included *Aetheorrhiza bulbosa* (L.) Cass., a species which Tausch, in failing to note its affinity with

Launea and *Sonchus*, had erroneously transferred to *Crepis* in 1828. But Bischoff excluded *Gatyona globulifera* Cass. (= *C. Dioscoridis* L.) from this group, and on the whole stood solidly with de Candolle and Lessing for the reduction in number of small genera. Bischoff alludes particularly to *Barkhausia* Moench, *Geracium* Rehb., *Intybus* Fries, *Aracium* Monn., and *Soyeria* Monn., as being inseparable from *Crepis*.

Only 15 years later C. H. Schultz Bipontinus swung the pendulum violently in the other direction. In one of his several papers (Pollichia 22-24: 311-322. 1866) he erects 4 subgenera for the disposition of 4 *Crepis* species, viz., *C. capillaris*, *C. tectorum*, *C. setosa*, and *C. vesicaria* subsp. *taraxacifolia*. These 4 species are to be found in 4 different sections in the present monograph; but, as is shown in Part I (p. 40), no satisfactory basis for the separation of *Crepis* into subgenera has been demonstrated. Schultz Bipontinus then proceeds to the recognition of 9 genera, all of which are now merged in *Crepis*, viz., *Wibelia* Gaertn., *Intybus* Fries, *Phaeacasium* Cass., *Brachyderca* Cass., *Berinia* Brignoli, *Aracium* Neck., *Omalocline* Cass., *Soyeria* Monn., and *Paleyia* Cass. Furthermore, under the last-named genus he included *Paleyia oligocephala* Sch. Bip. (*C. sibirica* Clarke non L.), a species which has recently been transferred to *Dubyaea* DC. by Stebbins (22), along with *Crepis bhotanica* Hutchinson (*C. Dubyaea* Marq. et Shaw) and *C. tsarongensis* Anthony. Commenting on the work of Schultz Bipontinus, Bentham (Jour. Linn. Soc. 13: 340. 1873) remarks: "His reliance chiefly upon the form of the achene for generic distinctions is in some cases a great improvement, in others carried so far as to be purely artificial. I must agree with him in his high estimation of the labours of Cassini; but that does not appear a sufficient reason for adding one more to the numerous names already given to the order." Thus, the pendulum swings back again in the work of Bentham.

Bentham and Hooker reviewed in 1873 about 130 species, mostly of the Northern Hemisphere in the Old World. They state that although at first sight these species appear to be separable into 3 cohorts of equal generic value, further observation indicates that many species are intermediate or ambiguous, and, thus, the genus is to be retained in its entirety. The 3 cohorts, *Barkhausia*, *Crepis*, and *Catonia* of Moench, are treated essentially as subgenera. But the distinctions between them are not clear, and the characters used have been found by the present author to be inadequate for systematic purposes. Included under **Barkhausia** are: *Paleyia* Cass., *Anthochytrum* Rehb. (= *Hostia* Moench), *Lagoseris* Link non M. B., *Psammoseris* Boiss., *Anisoderis* Cass., *Nemauchenis* Cass., and *Ceramioccephalum* Sch. Bip., which last should have been in the next. Under **Crepis**: *Gatyona* Cass., *Eucrepis* (= *Crepis* Cass.), *Brachyderca* Cass., and *Youngia* Cass., which last has been excluded from *Crepis* (Babcock and Stebbins, Carnegie Inst. Wash. Pub. No. 484. 1937). Under **Catonia**: *Omalocline* Cass. (including *Aetheorrhiza* Cass.), *Soyeria* Monn., *Aracium* Neck. (*C. paludosa*), *Intybellia* Monn. (including *Geracium* Rehb.), and *Anisorhamphus* DC. Except for the inclusion of *Aetheorrhiza* and *Youngia* and the exclusion of *Phaeacasium* Cass., *Pterotheca* Cass., *Lagoseris* M. B., and *Zacintha* (Tourn.) L., and except for the attempt to assemble the species into 3 subgenera, this treatment of the genus by Bentham and Hooker is in essential agreement with that of the present monograph; but it is, of course, entirely lacking in fitness from a phylogenetic standpoint.

In 1889, Hoffmann (in Engler u. Prantl, Pflanzenfamilien IV. 5: 373-374), enumerating about 170 species, recognized as *Crepis* the same former genera of Cassini and others that Bentham and Hooker did. He also included both *Aetheorrhiza* and *Youngia*, and under the latter he mentioned *Crepis glomerata*

(Dene.), which later became the type species of *Sorosseris* Stebbins (27–28). Apparently, Hoffmann recognized the difficulty in establishing subgenera in this genus, for he assembled the previously recognized genera into 9 sections. In attempting a systematic treatment of these sections, however, he used such trivial characters as length of pappus and presence or absence of a long beak on the achenes to differentiate the species. This resulted in placing such a primitive species as *C. hypochaeridea* (of sec. 8 in the present monograph) in the same section with *C. foetida* and *C. rubra* (of our sec. 20). In fact, a truly systematic treatment is practically nonexistent in Hoffmann's assemblage.

Further efforts at a systematic treatment of the whole genus have been entirely lacking until the present author undertook this one. The dispositions of parts of the group made in numerous floras have exhibited the two tendencies toward lumping and splitting mentioned above. For example, in 1904 the treatment by Fiori (428–442) is definitely conservative, although he did keep *Pterotheca* and *Zacintha* as genera. But he recognized only 3 major subgeneric groups in *Crepis*, distinguishing between them on the basis of achenial characters solely, a procedure which fails to distinguish the numerous natural subgroups in this genus. The following year Rouy published his treatment of the group, in which he recognized as genera *Barkhausia* Moench, *Crepis* L. (Gen. ed. 6, 914. 1764 emend.), *Soyeria* Monn., and *Pterotheca* Cass. These illustrations will suffice to indicate the need for a thorough monographic study of the genus, a need which has continued up to the present.

DIAGNOSIS

Crepis (Vaill.) L., Gen. ed. 1. 240. n. 621. 1737; Sp. Pl. 2: 805–808. 1753.

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- Anisoderis* Cass., Diet. 48: 429. 1827.
- Anisoramphus* DC., Prod. 7: 251. 1838.
- Anthochytrum* Rehb., Ic. Fl. Germ. 19: 39. t. 1432. 1859.
- Aracium* Neck., Elem. 1: 49. 1790.
- Barkhausia* Moench, Meth. 537. 1794.
- Barkhausenia* Hoppe, Flora 12: 512. 1829.
- Berinia* Brignoli, Pl. Forojul. 30. 1810.
- Billotia* Sch. Bip., in Herb. et Winck., Jahrb. Pharmac. 4: 155 in nota. 1841.
- Borkhausia* Nutt., Gen. Am. 2: 125. 1818.
- Brachyderea* Cass., Diet. 48: 429. 1827.
- Calliopea* Don, Edinb. N. Phil. Jour. 309 (Jan.–Mar.) 1829.
- Catonia* Moench, Meth. 535. 1794.
- Ceramiocephalum* Sch. Bip., Bull. Soc. Bot. Fr. 9: 284. 1862.
- Closirospermum* Neck., Elem. 1: 54. 1790.
- Crenamum* Adans., Fam. 2: 112. 1763.
- Crepinia* Rehb., in Moessl., Handb. 2: 1415. 1828.
- Crepidum* Tausch, Flora 11: 1. Erg. 80. 1828.
- Derouetia* Boiss., Diagn. ser. 2. 5: 114. 1856.
- Endoptera* DC., Prod. 7: 178. 1838.
- Galyona* Cass., Diet. 18: 184. 1820.
- Geracium* Rehb., ex Moessl., Handb. 2: 1345. 1828.
- Hapalostephium* Don, Edinb. N. Phil. Jour. 307. (Jan.–May) 1829.
- Hieraciodes* O. Kuntze, Gen. 1: 345. 1891.
- Homalocline* Rehb., Consp. 97. 1828.
- Hostia* Moench, Meth. Suppl. 221. 1802.

- Idianthes* Desv., Fl. Anj. 199. 1827.
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ORIGINAL DESCRIPTION

621. **Crepis**¹ Hieracioïdes Vaill. A. G. 1721. 47. 52. 13. 17. 18.

CAL: *Communis* auctus, oblongus: *Squamis multis* linearibus, aequalibus, parallelis. *S. paucis* brevibus, basi incumbentibus.

COR: *Composita* imbricata, uniformis: *corollulis hermaphroditis* plurimis, aequalibus. *Propria* monopetala, ligulata, linearis, truncata, quinquedentata.

STAM: *Filamenta* quinque, capillaria, brevissima. *Anthera* cylindracea, subulata.

PIST: *Germen* infra corollam propriam. *Stylus* filiformis, longitudine staminum. *Stigmata* duo, reflexa.

PER: nullum. *Calyx* subrotundus.

SEM: solitaria, oblonga, coronata *Pappo* longo, plumoso.

REC: nudum.

EXPANDED DESCRIPTION

Perennial, biennial, or annual herbs; plant \pm pubescent or glabrous; rhizomatous or with a deeply penetrating, woody or ephemeral root; caudex \pm woody, rarely suffruticulose, leafy; caudical leaves usually rosulate, many or few, persistent or ephemeral; cauline leaves numerous, few or none, the lower similar to the caudical ones or (sec. *Pyramachos*) cataphyllous, the others gradually or abruptly reduced, sometimes all or mostly bractlike; stem or stems erect or decumbent, \pm branched or

¹ *Crepis* Vaill. is referred to *Sonchus* Tourn. by Linnaeus (Gen. ed. 1. 240. no. 617. 1737).

scapiform; heads large, medium, or small, many- or few-flowered; involucre composed of outer and inner series of bracts, glabrous, tomentose, pubescent, setose, or hirsute; outer bracts many or few, up to $\frac{3}{4}$ as long as the inner bracts or very short, ovate-lanceolate and \pm imbricate to linear, remote; inner bracts in 2 or more ranks, many or few, glabrous or pubescent on inner face, in mature fruiting heads becoming little changed, or each bract becoming \pm carinate or navicular and spongy-thickened on outer face and then usually ultimately reflexed, or the whole involucre becoming strongly indurate enclosing the achenes; receptacle plain or convex, areolate and naked, or alveolate, the fimbriae often ciliate, or paleaceous with setiform or thin narrow membranous bracteiform paleae; corolla tubular-ligulate, the tube $\frac{1}{4}$ – $\frac{1}{2}$ (mostly $\frac{1}{3}$) as long as the whole corolla, the ligule yellow, orange, pink, or white, self-colored or tinged reddish or rarely greenish on the outer face, ligule teeth 5 or rarely 4, \pm glandular, sometimes purple; anther tube yellow, greenish, white, or pink, the appendages long or short, oblong-truncate to linear-acuminate; style branches filiform, attenuate, or truncate at the apex, yellow or green; achenes black, purplish, reddish, brown, tawny, yellow, stramineous, or white, monomorphic and all beakless or beaked, or dimorphic, the marginal compressed and the inner terete or the marginal beakless and the inner beaked, 10–35-ribbed or striate; pappus white, dusky, or yellow, uni- or multiseriate, the setae coarse or fine, rigid, pliable, or very soft, from extremely short (less than 1 mm) to longer than the achene, united at base or free, persistent, deciduous, or caducous.

The word *Crepis* (Κρηπίς) comes from the folk speech of the old Greeks, according to Bischoff (*op. cit.* 245), and is found as the name of a plant in Theophrastus (*Hist. lib. VI. cap. 8*). According to G. Dalla Fior (*La Nostra Flora. Trento. 518–519. 1926*) the word means a sandal and refers to the shape of the fruit. But according to I. Low (*Die Flora der Juden 3:162. 1924*) the word signifies *ein Gebäck* = a baking, a batch of baker's wares, or pastry, which probably refers to the symmetrical rosettes formed by the caudal leaves, and may be a modern connotation.

DIAGNOSES OF THE SECTIONS

Section 1.—**Desiphylion** sec. nov. Herbac perennes rhizomatosae; planta pubescens; folia infera magna petiolata; caulis robustus 3–15 dm altus oligocephalus; capitula magna multiflora; corolla 13–20 mm longa, tubo 3–9 mm longo; achaenia fusca vel straminea 4.5–11 mm longa 10–20-costata vel 25–35-striata; pappus albidus vel flavidus 6–10 mm longus.

Perennial rhizomatous herbs; plant pubescent; caudex leafy, 1-stemmed; lower leaves large, petiolate, dentate, or subpinnatifid; upper leaves gradually reduced, sessile; stem stout, 3–15 dm high, few-headed, aggregate inflorescence cymose-corymbiform; heads large or medium, many-flowered; longest outer involueral bracts $\frac{1}{4}$ – $\frac{2}{3}$ as long as the inner; inner bracts little changed in mature fruiting heads, glabrous on inner face; corolla 13–20 mm long, the tube 3–9 mm long; achenes brown, tawny, or stramineous, 4.5–11 mm long, fusiform or columnar, \pm attenuate, not beaked, 10–20-ribbed or 25–35-striate; pappus whitish or yellowish, 6–10 mm long. *Desiphylion*, from *desis*, a bond, + *phylon*, a tribe; indicating a connecting group. Type species: *C. sibirica* L.

Section 2.—**Spathoides** sec. nov. Herba perennis rhizomatosa; planta pubescens; folia oblanceolata petiolata denticulata; caulis robustus 3 dm altus oligocephalus; capitula magna 50-flora; corolla 14 cm longa, tubo 3–4 mm longo; achaenia nigra 6–7 mm longa, 10–12-costata; pappus albidus 7–8 mm longus.

Perennial rhizomatous herb; plant \pm pubescent, villous on upper leaves, peduncles, and involucre; caudex leafy, 1–2-stemmed; lower leaves oblanceolate, petiolate, denticulate, upper leaves gradually reduced, sessile; stem rather stout, about 3 dm high, 3–4-branched near the top, the branches pedunculate; heads large, up to 50-flowered; longest outer involueral bracts about $\frac{1}{2}$ as long as the inner; inner bracts becoming indurate but otherwise little changed at maturity, glabrous on inner face; corolla about 14 mm long, the tube 3–4 mm long; achenes blackish, 6–7 mm long, columnar, \pm attenuate, not beaked, 10–12-ribbed, the rounded ribs very prominent; pappus dusky white, 7–8 mm long. *Spathoides*, from *spathe*, a blade, + *-o* + *eidōs*, resembling; referring to the bladelike leaves. Type species: *C. kashmirica* Babe.

Section 3.—**Omalocline** (Cass., Dict. 48: 431. 1827 pro genus). Perennial rhizomatous herb; plant tomentose or tomentulose and sometimes gland-pubescent; caudex leafy, sometimes several-stemmed; leaves rather small, long-petiolate, lyrate-pinnately parted with few lateral lobes or these sometimes absent, upper leaves only slightly reduced; stems slender, 0.4–2 dm high, several-branched, the branches mostly pedunculate; heads medium, 40–50-flowered; longest outer involueral bracts $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner; inner bracts little changed in fruiting heads, sometimes spongy-thickened at the very base, glabrous on inner face; corolla 15–20 mm long, the tube 5–7 mm long; achenes dark or light brown or stramineous, 4–9 mm long, columnar, slightly attenuate to both ends, not beaked, 20–25-ribbed; pappus whitish or tawny, 7–10 mm long. *Omalocline*, from *homalos*, flat, + *klinē*, a bed; referring to the mat-forming habit. Type species: *C. pygmaea* L.

Section 4.—**Brachypodes** sec. nov. Herbae perennes; rhizoma praemorsa; planta pubescens; folia pinnatifida vel dentata petiolata; caulis 0.2–3 dm altus scapiformis vel furcatus bicephalus; capitula magna vel medioeria multiflora; corolla 12–25 mm longa, tubo 3–8 mm longo; achaenia fusca purpurea vel straminea 3–8 mm longa 10–20-costata; pappus albus vel flavidus 4–8 mm longus.

Perennial herbs; rhizome praemorse; plant pubescent; caudex leafy, 1–8-stemmed; lower leaves pinnatifid or dentate, petiolate, upper leaves gradually or abruptly reduced, sessile; stem or stems rather slender but strong, 0.2–2 (3) dm high, mostly scapiform and 1-headed, sometimes furcate, rarely more than 2-headed; heads large or medium, many-flowered (in *C. diorctica* 15–20-flowered); longest outer involueral bracts $\frac{1}{2}$ – $\frac{2}{3}$ ($\frac{3}{4}$) as long as the inner (in *C. aurea* sometimes $\frac{1}{3}$); inner bracts little changed at maturity, glabrous or pubescent on inner face; corolla 12–25 mm long, the tube 3–8 mm long; achenes dark or pale brown, purplish or stramineous (in *C. terglouensis* yellow, speckled with black or purple), 3–8 mm long, fusiform or columnar, not beaked (in *C. hokkaidoensis* attenuate into a neck or very coarse beak), 10–20-ribbed; pappus white, cream, or pale yellowish, 4–8 mm long. *Brachypodes*, from *brachys*, short, + *pous*, *podos*, a foot; referring to the short rhizome. Type species: *C. terglouensis* (Haeq.) A. Kern.

Section 5.—**Mesomeris** sec. nov. Herbae perennes rhizomatosae; planta pubescens; folia petiolata lyrato-pinnatifida vel integra; caulis robustus vel tenuus oligocephalus; capitula medioeria vel parva 25–100-flora; corolla 9–18 mm longa, tubo 2–5 mm longo; achaenia fusca 4–6 mm longa 10–20-costata vel 20-striata; pappus albus vel fuscidulus 4–7 mm longus.

Perennial rhizomatous herbs; plant pubescent; caudex leafy, 1- or several-stemmed; lower leaves petiolate, lyrate-pinnatifid, or entire; upper leaves gradually or abruptly reduced, sessile; stem or stems fairly robust to slender, few-branched, the branches mostly above the middle; few-headed, inflorescence cymose-corymbiform; heads medium to small, 25–100-flowered; longest outer involueral bracts $\frac{1}{4}$ – $\frac{3}{4}$ as long as the inner; inner bracts becoming carinate dorsally and \pm spongy-thickened near the base, glabrous on inner face; corolla 9–18 mm long, the tube 2–5 mm long; achenes brown or dark brown, 4–6 mm long, fusiform or columnar, slightly or moderately attenuate to both ends, not beaked, 10–20-ribbed or 20-striate; pappus white, dusky white, or pale tawny, 4–7 mm long. *Mesomeris*, from *mesos*, middle, + *meros*, a part; indicating its intermediate phyletic position. Type species: *C. lapsanoides* (Gouan) Tausch.

Section 6.—**Soyeria** (Monn., Essai Hierac. 74. 1829 pro genus, excl. *C. lapsanoides*; *Hapalostephium* Don, Edinb. N. Phil. Jour. 1829: 307). Perennial herbs; plant \pm pubescent, the involueres villous or hirsute; root woody, elongated into a taproot; caudex leafy, mostly 1-stemmed; lower leaves broadly to narrowly oblanceolate, entire, dentate or pinnatifid, petiolate; upper leaves gradually reduced, sessile; stem rather stout, 0.2–6 dm high, 1–2-headed or (*C. conyzaeifolia*, *C. blattarioides*) sometimes 3–6-branched, the branches mostly pedunculate; heads large or medium, many-flowered; longest outer involueral bracts $\frac{1}{2}$ – $\frac{3}{4}$ as long as the inner; inner bracts becoming indurate, otherwise not changed at maturity, pubescent or (*C. blattarioides*) glabrous on inner face; corolla 13–25 mm long, the tube 5–8 mm long; achenes tawny or brown, 5–12 mm long, columnar or fusiform, more attenuate toward the apex or equally attenuate to both ends, 15–20-ribbed, the ribs unequal or all narrow; pappus from pale tawny or yellowish to white, 5–9 mm long. *Soyeria*, derivation obscure. Type species: *C. pontana* (L.) Dalla Torre.

Section 7.—**Paleyia** (Cass., Dict. 39: 393. 1826 pro genus). Perennial herbs; plant pubescent; root woody, elongated into a taproot; caudex woody, thickened, sometimes suffruticulose, leafy, mostly 1-stemmed; lower leaves oblanceolate or (*C. albida scorzonoides*) elliptic, denticulate, dentate, or pinnatifid; upper leaves few, \pm reduced, sessile; stem or stems erect, 0.4–12 dm high, 1-headed or few-branched, several-headed; heads large or medium, many-flowered; outer involueral bracts \pm imbricate, the longest $\frac{1}{2}$ – $\frac{3}{4}$ as long as inner bracts in fruiting heads; inner bracts pubescent or glabrous on inner face, becoming carinate dorsally and indurate but little if at all thickened at maturity; corolla 14–22 mm long, the tube 4–9 mm long; achenes stramineous, yellow, tawny, or light brown, 8–18 mm long, fusiform, gradually long-attenuate or definitely beaked, 10–20-ribbed, the ribs narrow; pappus white, whitish, or tawny, 4–11 mm long. *Paleyia*, derivation obscure. Type species: *C. albida* Vill.

Section 8.—*Anisorhamphus* (DC., Prod. 7: 251. 1838 pro genus). Perennial herbs; plant pubescent; root woody, elongated into a taproot; caudex woody, thickened, sometimes suffruticose, leafy, 1- or several-stemmed; lower leaves oblanceolate, petiolate, denticulate, dentate, or rarely subpinnatifid; upper leaves lanceolate, sessile, gradually reduced and rather conspicuous or abruptly reduced and small or bractlike; stem or stems erect, 0.3–15 dm high, few-branched and few- or several-headed, or sometimes 1-headed; heads large or medium, many-flowered; outer involucre bracts not imbricate or (*C. scaposa tarazaciformis*, *C. glandulosissima*) imbricate, the longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner or (*C. Friestii*) absent or displaced to summit of peduncle; inner bracts setulose or \pm gland-pubescent on outer face, glabrous or pubescent on inner face, little changed in fruiting heads or rarely somewhat spongy-thickened near the base; corolla 6–23 mm long, the tube 1.5–7 mm long; achenes of various shades of brown, 4–11 mm long, fusiform, attenuate to the apex or definitely beaked, the beak short or equal to the body, coarse or medium, 10–20-ribbed, the ribs narrow, sometimes rather prominent; pappus pale yellow, yellowish-white, or rarely white, 4–10 mm long. *Anisorhamphus*, from *anisos*, unequal, + *rhamphos*, a beak; referring to the achenes of some species. Type species: *C. hypochaeridea* (DC.) Thell.

Subsection A.—*Amplifoliatae* subsec. nov. Folia caudicalia longa cauline magna; caulis plerumque ramosus; involucre setosa vel setulosa, setis nigris plerumque eglandulosis.

Caudical leaves long in proportion to height of the plant; cauline leaves relatively large and conspicuous; stems not scapiform, or if 1-headed (*C. alpestris*), the cauline leaves conspicuous; involucre setose or setulose, the setae or setules black and mostly glandless, or if glandular (*C. alpestris*, *C. suffruticosa*), the stems leafy. Type species: *C. kilmandscharica*. O. Hoffm.

Subsection B.—*Parvifoliatae* subsec. nov. Folia caudicalia plerumque brevia caulina parva; caulis scapiformis vel ramosus bracteatus; involucre pubescentia, pilis plerumque glandulosis.

Caudical leaves short in proportion to height of the plant, or if sometimes relatively long (*C. scaposa*, *C. ugandensis*), then the stems scapiform or branched but merely bracteate; cauline leaves mostly small, bractlike; involucre shortly gland-pubescent or sometimes gland-setulose or, if setulose and glandless (*C. Gossweileri*), the basal leaves small and the stem leaves bractlike. Type species: *C. urundica* Bab.

Section 9.—*Gephyroides* sec. nov. Herbae perennes vel annuae; radix lignea robusta vel tenua elongata; caudex carnosus elongatus vel ligneus brevis; folia infera spathulata vel oblanceolata dentata vel pinnatifida; caules 1–4 dm alti tenui, capitulis paucis vel multis; capitula magna medioeria vel parva multiflora; corolla 9–15 mm longa, tubo 2–4 mm longo; achaenia fusca 2–8 mm longa fusiformia attenuata vel breve rostrata 10-costata; pappus albus vel albidus 3–6 mm longus.

Perennial or annual herbs; plant glabrous or \pm pubescent or setulose; root strong, woody, persisting, or slender, not persisting, usually elongated into a taproot; caudex fleshy or woody, elongated or short, 1–8-stemmed; lower leaves spatulate or oblanceolate, dentate to bipinnatifid, the others similar or sessile, gradually reduced; stem or stems 1–4 dm high, slender, erect or sometimes semidecumbent, few- or many-headed; heads large, medium, or small, many-flowered; longest outer involucre bracts $\frac{1}{4}$ – $\frac{1}{2}$ as long as the inner; inner bracts becoming carinate and spongy-thickened, pubescent or glabrous on inner face; corolla 9–15 mm long, the tube 2–4 mm long; achenes brown, 2–8 mm long, fusiform, attenuate to the apex, with or without a short coarse or fine beak; 10-ribbed; pappus white or whitish, 3–6 mm long. *Gephyroides*, from *gephyra*, a bridge, + *-oides*, resembling; figuratively a bridging group. Type species: *C. tingitana* Salz.

Section 10.—*Berinia* (Brignol., Pl. Forojul. 50. 1810 pro genus, excl. spp. Schultz Bipontini; *Brachyderea* Cass., Dict. 48: 429. 1827). Perennial herbs; plant \pm pubescent or glabrescent; root woody, elongated into a taproot; caudex woody, simple or sometimes furcate, leafy, mostly 1-stemmed, in a few species several-stemmed; lower leaves oblanceolate, petiolate, denticulate, dentate, or pinnatifid (in *C. crocifolia* linear, entire); upper leaves lanceolate or elliptic, sessile, gradually reduced and conspicuous or abruptly reduced and small or bractlike; stem or stems erect or spreading, 0.5–12 dm high, few-branched and few-headed or several-branched and several- or many-headed; heads large, medium, or rarely small, 11–100-flowered; outer involucre bracts not imbricate, the longest $\frac{1}{4}$ – $\frac{1}{2}$ as long as the inner; inner bracts setose, pubescent or tomentose on outer face, glabrous, pubescent or strigulose on inner face, becoming \pm carinate and indurate or spongy-thickened in fruit; corolla 12–21 mm long, the tube 2–10 mm long; achenes brown, brownish, yellowish, stramineous, or orange, 4–9 mm long, fusiform, \pm attenuate or rarely with a short coarse beak, 10–30-ribbed or -striate, the ribs or striae medium to narrow, nearly equal or sometimes with several stronger ones; pappus white, whitish, or rarely yellowish, 4–9 mm long. *Berinea*, perhaps from *Beroë*, a nymph, + *-inos*, denoting source. Type species: *B. andryaloides* Brignol. = *C. chondriloides* Jacq.

Subsection C.—**Corymbiformae** subsec. nov. Planta 2–12 dm alta; folia caudicalia ampla elliptica vel oblanceolata; folia caulina plerumque numerosa conspicua lanceolata vel elliptica; caulis robustus paniculatus; inflorescentia corymbiformis vel racemiformis; capitula magna vel medioeria 12–100-flora; involucria setosa vel pubescentia vel tomentosa.

Plant 2–12 (mostly 3–6) dm high; caudical leaves broad, elliptic or oblanceolate; cauline leaves usually numerous, gradually reduced, conspicuous, lanceolate or elliptic; stems robust, paniculately branched; inflorescence corymbiform or racemiform; heads large or medium, 12–100-flowered; involucria setose, pubescent with or without glands, or tomentose. Type species: *C. pannonica* (Jacq.) Koch.

Subsection D.—**Subcorymbiformae** subsec. nov. Planta 1–4.5 dm alta; folia caudicalia ampla oblanceolata; folia caulina plerumque parva bracteiformia; caulis rectus robustiusculus vel tenuis furcatus; inflorescentia subcorymbiformis; capitula medioeria vel magna 50–80-flora; involucria tomentosa saepe pubescentia.

Plant 1–4.5 dm high; caudical leaves broad, oblanceolate; cauline leaves mostly small, bractlike; stem erect, rather stout or slender, 1–3-furcate; inflorescence subcorymbiform; heads medium or large, 50–80-flowered; involucria \pm tomentose, often pubescent. Type species: *C. auriculaefolia* Sieber.

Subsection E.—**Divaricatae** subsec. nov. Planta 0.3–5 dm alta; folia caudicalia ampla oblanceolata; folia caulina plerumque parva bracteiformia; caulis tenuis furcatus, ramis paucis divaricatis; inflorescentia diffusa; capitula medioeria 15–80-flora; involucria tomentosa interdum pubescentia vel setulosa.

Plant 0.3–5 (mostly 1–3.5) dm high; caudical leaves broad, oblanceolate; cauline leaves mostly small, bractlike; stem slender, furcate, divaricately few-branched; inflorescence diffusely cymose; heads medium, 15–80-flowered; involucria tomentose, sometimes pubescent or setulose. Type species: *C. Raulini* Boiss.

Subsection F.—**Strictae** subsec. nov. Planta 1.5–4.5 dm alta; folia caudicalia linearia vel anguste oblanceolata; folia caulina similia gradatim reducta; caules tenui ramosi, ramis paucis elongatis strictis; inflorescentia cymosa; capitula magna medioeria vel parva 11–40-flora; involucria tomentosa vel pubescentia.

Plant 1.5–4.5 dm high; caudical leaves linear or narrowly oblanceolate; cauline leaves similar, gradually reduced; stems slender, few-branched, the branches elongated, strict; inflorescence cymose; heads large, medium, or small, 11–40-flowered; involucria tomentose or pubescent. Type species: *C. turcomanica* H. Krasch.

Section 11.—**Macropodes** sec. nov. Herbae perennes; planta pubescens; radix robusta lignea elongata; caudex ligneus simplex vel furcatus foliatus; folia infera oblanceolata dentata vel pinnatifida petiolata; folia superna bracteiformia; caules 0.2–3.5 dm alti tenui scapiformes vel 1-furcati cum 2–4 capitulis; capitula medioeria vel parva 11–60-flora; corolla 10–18 mm longa, tubo 2.5–6.5 mm longo; achaenia straminea fusca vel nigra 4–9.5 mm longa 10–20-costata vel -striata; pappus albus flavidulus vel fuscidulus 3–8 mm longus.

Perennial herbs; plant pubescent; root stout, woody, elongated into a taproot; caudex leafy, 1- or several-stemmed; lower leaves oblanceolate, denticulate, dentate, pinnatifid or bipinnate, petiolate; upper leaves all or mostly bractlike; stem or stems slender, scapiform, 1-headed, or sometimes furcate and 2- or rarely 3–4-headed; heads medium or small, with 11–60 or more florets; longest outer bracts $\frac{1}{4}$ – $\frac{2}{3}$ (mostly $\frac{1}{8}$ – $\frac{1}{2}$) as long as the inner; inner bracts becoming convex and indurate or slightly thickened but otherwise little changed at maturity, or becoming definitely carinate and spongy-thickened dorsally, glabrous or pubescent on inner face; corolla 10–18 mm long, the tube 2.5–6.5 mm long; achenes ranging in color from stramineous or pale brown to dark brown, dark purple, or black, 4–9.5 mm long, fusiform or columnar, sometimes strongly attenuate or rarely shortly beaked, 10–20-striate or -ribbed, the striae or ribs unequal or equal; pappus white, yellowish, or tawny, 3–8 mm long. Macropodes, from *makros*, long, + *pous*, *podos*, a foot; referring to the long taproot. Type species: *C. oreades* Schrenk.

Section 12.—**Ixeridopsis** sec. nov. Herbae perennes; planta glabra; radix tenuis lignea elongata; caudex tenuis ligneus simplex vel furcatus interdum elongatus foliatus; folia infera ovata elliptica vel oblanceolata sessilia vel petiolata integra denticulata dentata vel subpinnatifida; folia superna similia vel bracteiformia; caules 0.2–3.5 dm alti tenni ramosi; inflorescentia corymbiformis vel diffusa; capitula medioeria vel parva 6–13-flora; involucrium cylindricum tenue glabrum, squamis exterioribus 5–8 ovatis brevissimis, interioribus 8–10 lanceolatis 3–7-plo longioribus; receptaculum nudum; corolla 7–14 mm longa, tubo 2.5–5 mm longo; achaenia straminea vel fusca 4–8 mm longa teretia ad summitatem paululum attenuata vel bressime rostrata 10-costata vel -striata; pappus albus vel flavidus 4–6.5 mm longus.

Perennial herbs; plant glabrous; root slender, woody, elongated into a taproot; caudex slender, woody, simple or furcate, sometimes much elongated and branched, leafy; lower leaves ovate,

elliptic or oblanceolate, sessile or petiolate, entire, denticulate, dentate or subpinnatifid, upper leaves similar or bractlike; stems 0.2–3.5 dm high, slender, branched; inflorescence corymbiform or diffuse; heads medium or small, 6–13-flowered; involucre cylindric, narrow, glabrous; outer bracts 5–8, ovate, very short, the longest $\frac{1}{4}$ – $\frac{1}{3}$ as long as the inner; inner bracts 8–10, lanceolate; receptacle naked; corolla 7–14 mm long, the tube 2.5–5 mm long; achenes stramineous or brownish, 4–8 mm long, terete, \pm attenuate or shortly beaked, 10-ribbed or -striate; pappus white or yellowish, 4–6.5 mm long. *Ixeridopsis*, from *Ixeris*, a genus of plants, + *opsis*, appearance. Type species: *C. nana* Richards.

Section 13.—*Intybellia* (Monn., Essai Hierac. 78. 1829 pro genus, excl. *C. pulchra* L.; non Cass.; *Intybellioides* DC., Prod. 7: 164. 1838 pro parte). Perennial rhizomatous herbs; plant pubescent; caudex leafy, 1-stemmed; lower leaves petiolate, oblanceolate or obovate, denticulate or dentate; upper leaves all or mostly bractlike; stem slender, fistulose, branched near the summit, the inflorescence cymose-corymbiform or racemiform; heads medium or small, 10–50-flowered; longest outer involucre bracts $\frac{1}{3}$ – $\frac{2}{3}$ as long as the inner; inner bracts becoming carinate dorsally and pale spongy-thickened near the base, glabrous on inner face; corolla 9–15 mm long, the tube 3–4.5 mm long; achenes light brown, 4–5.5 mm long, fusiform, \pm attenuate to both ends, not beaked, about 20-ribbed; pappus white, 3.5–6 mm long. *Intybellia*, from Latin *intybus*, chicory, + *ell*, diminutive. Type species: *C. incarnata* (Wulf.) Tausch.

Section 14.—*Mesophyllion* sec. nov. Herbae perennes; planta glabrescens puberula vel pubescens; radix tenua elongata; folia petiolata oblanceolata vel lanceolata denticulata dentata vel pinnatifida; caulis tenuus vel crassiusculus fistulosus cymose ramosus; capitula magniuscula vel parva 30–75-flora; corolla 9–17 mm longa, tubo 3–6 mm longo; achaenia fusco-purpurascens 2.5–8 mm longa fusiformia erostrata 10–12-costata; pappus albus 4–8 mm longus.

Perennial or annual herbs; plant glabrescent, puberulent or pubescent; root slender, elongated into a taproot; caudex leafy, 1-stemmed; lower leaves petiolate, oblanceolate or lanceolate, denticulate, dentate or pinnatifid; upper leaves small, linear or bractlike; stem slender to stout, fistulose, paniculately branched, the inflorescence mostly cymose-corymbiform; heads rather large to small, 30–75-flowered; longest outer involucre bracts $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner; inner bracts at maturity becoming somewhat thickened and indurate or \pm carinate and spongy-thickened dorsally, pubescent or glabrous on inner face; corolla 9–17 mm long, the tube 3–6 mm long; achenes dark reddish or purplish-brown, 2.5–8 mm long, fusiform, \pm attenuate, not beaked, 10–12-ribbed; pappus white, 4–8 mm long. *Mesophyllion*, from *mesos*, middle, + *phylon*, a tribe; referring to interconnecting relationships. Type species: *C. Bungei* Ledeb.

Section 15.—*Psilochaenia* (Nutt., Trans. Am. Phil. Soc. n.s. 7: 436. 1840 pro genus). Perennial herbs; plant tomentose, tomentulose, glabrescent or rarely glabrous; root slender or stout, elongated into a taproot or rarely branched near the caudex and \pm fibrous; caudex leafy, 1–4-stemmed; lower leaves petiolate, obovate, oblanceolate, elliptic, lanceolate or linear, entire, denticulate, dentate, pinnatifid or bipinnatifid; upper leaves mostly sessile, gradually reduced, or mostly small, linear or bractlike; stem slender to stout, cymosely branched, the inflorescence mostly corymbiform; heads large to small, 4–60-flowered; longest outer involucre bracts $\frac{1}{2}$ – $\frac{3}{4}$ as long as the inner; inner bracts at maturity becoming more or less carinate and spongy-thickened dorsally, strigulose, pubescent or glabrous on inner face; corolla 10–30 mm long, the tube 3.5–10 mm long; achenes of various colors, 3–12 mm long, columnar, fusiform, rarely coarsely beaked, 10–18-ribbed; pappus white, dusky, or yellowish-white, 4–13 mm long. *Psilochaenia*, from *psilos*, smooth, + *achanē*, achene. Type species: *C. occidentalis* Nutt.

Section 16.—*Lagoseris* (M. B., Fl. Taur. Cauc. 3: 538. 1819 pro genus; non Hoffmeigg. et Link, Fl. Port. 2: 149. 1820 = *Intybellia* Cass., Bull. Philom. 1821: 124, non Monn.). Perennial herbs; plant pubescent or tomentose, or the leaves glabrous; caudex arising from a subterranean shoot or elongated into a vertical taproot, simple or divided, leafy at crown; lower leaves petiolate, oblanceolate, lanceolate or rarely spatulate, denticulate, dentate, pinnatifid or bipinnatifid; upper leaves sessile, gradually reduced, or mostly small, linear or bractlike; stem tall, paniculately branched, or stems 1–6, low, slender, 1–3-furcate or scapiform; heads medium, many-flowered; longest outer involucre bracts $\frac{1}{3}$ – $\frac{2}{3}$ as long as the inner; inner bracts at maturity becoming more or less carinate and spongy-thickened dorsally, mostly glabrous on inner face; receptacle paleaceous, the paleae setiform, sometimes exceeding the pappus; corolla 10–16 mm long, the tube 2.5–4.5 mm long; achenes monomorphic, brown or stramineous, fusiform or columnar, 4.5–8.5 mm long, 10–20-ribbed; pappus white, 4–5 mm long. *Lagoseris*, from *lagos*, a hare, + *seris*, endive or lettuce. Type species: *C. purpurea* (Willd.) M. B.

Section 17.—*Napiseris* sec. nov. Herba perennis; planta pubescens; radix napiformis vel columnaris lignea vel carnosae; folia petiolata oblanceolata vel elliptica denticulata dentata vel pinnatifida; caulis elatus ad summitatem ramosus, ramis brevissimis, capitulis congestis; inflorescentia racemiformis; capitula parviuscula 5–10-flora; corolla flava circa 11 mm longa,

tubo 4 mm longo; achaenia fusca 4 mm longa fusiformia erostrata 10-costata; pappus flavus 4 mm longus.

Perennial herb; plant pubescent; root vertical, napiform or columnar, woody or somewhat fleshy; caudex simple or divided, narrow, leafy; lower leaves petiolate, oblanceolate or elliptic, denticulate to shallowly lobed; upper leaves mostly small, linear or bractlike; stem tall, woody, branched toward summit, the branches short, each with several heads in a congested cluster, the aggregate inflorescence paniculate-racemiform; heads rather small, 5-10-flowered; longest outer involucre bracts $\frac{1}{4}$ - $\frac{1}{2}$ as long as the inner ones and, like them, medio-dorsally nerved, the nerve thickened or tuberculate near the apex; inner bracts 5 or 6, glabrous on inner face; corolla about 11 mm long, the tube about 4 mm; achenes brown, gradually attenuate, not beaked, subterete or obscurely angled, 3.5-4.5 mm long, 10-ribbed; pappus yellow, 4 mm long. Napiseris, from Latin *napus*, a turnip, + *seris*, endive or lettuce; referring to the napiform root. Type species: *C. napifera* (Franch.) Babe.

Section 18.—**Pyramachos** sec. nov. Herbae perennes; planta glabra vel pubescens; radix lignea elongata; caudex vivax simplex vel ramosus non foliatus; folia caulina infera squamiformia parva triangularia acuta, altera gradatim sursum crescens lanceolata vel linearia acuta vel acuminata; caulis erectus tenuis ligneus, ramis fastigiatis strictis vel anguste divaricatis; inflorescentia cymose corymbiformis; capitula parva vel media 7-25-flora; corolla 10-15 mm longa, tubo 3-4 mm longo; achaenia fusca fusiformia erostrata vel breve rostrata 3.5-5 mm longa 10-16-costata; pappus albus vel flavidulus 3-6 mm longus.

Perennial herbs with glabrous or pubescent foliage; caudex slender but strong, woody, elongated into a taproot, simple or divided at the crown; lowest cauline leaves or cataphylls inconspicuous, triangular, acute, scalelike, persisting, the other cauline leaves gradually increasing, reaching maximum size near or above the mid-region, middle and upper cauline leaves narrowly lanceolate to filiform, acute or acuminate, sessile, the margins retrorsely revolute; stem or stems erect, woody, branched, the branches fastigate, strict or somewhat divaricate; aggregate inflorescence cymose-corymbiform; heads small to medium, 7-25-flowered; involucre cylindric-campanulate; outer bracts unequal, the longest $\frac{1}{4}$ - $\frac{2}{3}$ as long as the inner, narrow, not imbricate; inner bracts glabrous on inner face, at maturity dorsally carinate and thickened at the base; receptacle naked; corolla 10-15 mm long, the tube 3-4 mm long; achenes brown, fusiform, subterete or subcompressed, sometimes shortly and coarsely beaked, 3.5-5 mm long, 10-16-ribbed; pappus white or cream-colored, 3-6 mm long. *Pyramachos*, from *pyr*, fire, + *machē*, combat; referring to fire resistance. Type species: *C. Phoenix* Dunn.

Section 19.—**Phaecasium** (Cass., Dict. 39: 787. 1826 pro genus; *Idianthes* Desv., Fl. Anj. 199. 1827; *Sclerophyllum* Gaud., Fl. Helv. 47. 1829). Perennial or annual herbs; plant pubescent; root elongated into a slender taproot; caudex broad or narrow, leafy; lower leaves petiolate, oblanceolate or obovate, dentate to pinnatifid; upper leaves sessile, lanceolate or mostly reduced, linear or bractlike; stem or stems erect, usually branched, the lower branches elongated, aggregate inflorescence corymbiform; heads medium or small, 15-65-flowered; longest outer involucre bracts $\frac{1}{4}$ - $\frac{2}{3}$ or rarely $\frac{1}{2}$ as long as the inner; inner bracts pubescent or glabrous on inner face, at maturity strongly carinate and spongy-thickened dorsally; corolla 5-19 mm long, the tube 2-6.5 mm long; achenes of 1, 2, or 3 shapes, tawny, greenish-yellow, or brown, erostrate or (*C. pterothecoides*) mostly beaked, 3-10 mm long, 10-20-ribbed or striate; pappus white, 3-6 mm long, extremely fine. *Phaecasium*, probably from *phaikos*, spendid, + *sim*, a kind of meadow plant. Type species: *C. pulchra* L. (= *P. lampsanoides* Cass., loc. cit.).

Section 20.—**Hostia** (Moench. Meth. Suppl. 221. 1802 pro genus non Jacq., Pers., Willd.; *Anisoderis* Cass., Dict. 48: 429. 1827 pro parte). Annual or sometimes biennial herbs; plant pubescent or hispid; root generally slender, with a fine taproot, occasionally thickened and woody; caudex usually simple, 1-stemmed, rarely divided, several-stemmed; lower leaves mostly petiolate, oblanceolate, or obovate-oblong or lanceolate to linear, denticulate to bipinnatifid; upper leaves mostly sessile, lanceolate, gradually reduced, often lacinate near the base, or mostly if not all small and bractlike; stem or stems erect or ascending, usually branched, the lower branches elongated, with the inflorescence corymbiform, or the stems scapiform, 1-headed; heads mostly large or medium, rarely medium to small, erect or nodding before anthesis, 40-114-flowered; longest outer involucre bracts $\frac{1}{4}$ - $\frac{2}{3}$ as long as the inner; inner bracts pubescent, strigose, or rarely glabrous on inner face, at maturity strongly carinate, enclosing marginal achenes, becoming indurate or usually spongy-thickened toward the base; corolla 7-19 mm long, the tube 3-7 mm long; achenes 5-21 mm long, of 1 or 2 shapes, the inner ones always long-beaked and with 10-20 fine ribs or striae, the marginal shorter, mostly paler in color, often thicker and beakless; pappus yellowish or whitish, 3-8 mm long. *Hostia*, derivation obscure. Type species: *C. foetida* L.

Section 21.—*Microcephalum* sec. nov. Herbae perennes; planta pubescens vel hispidulosa; caudex rhizomatosus elongatus vel praemorsus simplex vel furcatus foliatus; folia infera oblanceolata vel elliptica petiolata dentata vel pinnatifida; folia supera pauca parva vel bracteiformia; caules 1-9 erecti tenui vel crassiusculi, ramis paucis; capitula parva 20-40-flora; corolla 6.5-14 mm longa, tubo 2.5-5 mm longo; achaenia aureo-rubro- vel nigro-fusca 4-5 mm longa fusiformia 10-12-costata, costis tenuis; pappus albus 4-6 mm longus.

Perennial rhizomatous herbs; plant pubescent or hispidulous; rhizome horizontal, oblique or praemorse, fibrillate; caudex simple or furcate, leafy at crown; lower leaves oblanceolate or elliptic, petiolate, dentate or pinnatifid; upper leaves few, mostly reduced, linear or bract-like; stems 1-9, erect, slender or (*C. tibetica*) rather stout, few-branched, the branches few-headed; heads small, 20-40-flowered; longest outer involucre bracts very short or $\frac{1}{4}$ - $\frac{1}{2}$ as long as the inner; inner bracts glabrous on inner face, becoming \pm spongy-thickened toward the base in fruit; corolla 6.5-14 mm long, the tube 2.5-5 mm long; achenes monomorphic, golden, reddish, or dark brown, 4-5 mm long, narrowly fusiform, 10-12-ribbed; pappus white, 4-6 mm long. *Microcephalum*, from *mikros*, small, + *kephalē*, a head; referring to small flower heads. Type species: *C. Gmelini* (L.) Tausch.

Section 22.—*Pterotheca* (Cass., Bull. Soc. Philom. 1816: 200; *op. cit.* 1821: 125; Dict. 44: 56. 1826; cf. tab. in *op. cit.* 25: 62, 1823 pro genus, based on *P. nemausensis* Cass. = *C. sancta* subsp. *nemausensis*). Annual herb; plant pubescent; root slender, ephemeral; caudex leafy; lower leaves rosulate, obovate, oblanceolate or spatulate, petiolate, denticulate, dentate or pinnatifid; upper leaves few, reduced, linear or bractlike; stem or stems semidecumbent, strict or erect, very slender to robust, simple or dichotomously or cymosely branched, few- or many-headed; heads medium to small, 30-60-flowered; outer involucre bracts nearly equal, ovate to linear, white-margined; inner bracts glabrous on inner face, strongly carinate and spongy-thickened on outer face in fruit; receptacle paleaceous, the paleae setiform; corolla 7-13 mm long, the tube $\frac{1}{4}$ - $\frac{1}{3}$ as long; achenes triformic, the outermost (sometimes absent) paler, from strongly alate to 3-angled or with 3 stronger ribs, the innermost terete, slender, smooth, the intermediate ones terete, coarsely or finely spiculate; pappus white, scarcely exceeding the involucre. *Pterotheca*, from *pteron*, a wing, + *thēkē*, a box; referring to the winged achenes. Type species: *C. sancta* (L.) Bab.

Section 23.—*Zacintha* ([Tourn.] L., Syst. ed. 1. 1735; Gaertn., Fruct. 2: 358. t. 157, 1791 pro genus). Perennial or annual herbs; plant pubescent or the leaves glabrous; root stout, woody or slender, ephemeral; caudex leafy; lower leaves rosulate, often disappearing early, oblanceolate, denticulate, runcinate or lyrate-pinnatifid; upper leaves mostly sessile, reduced or bract-like; stem erect, the central axis stronger than the branches, or very short and slender, divaricately branched above or from near the base, the branches strict or decumbent, few- or many-headed; heads medium or small, 25-70-flowered; outer involucre bracts $\frac{1}{3}$ - $\frac{2}{3}$ as long as the inner; inner bracts pubescent or glabrous on inner face, remaining erect and becoming \pm indurate, enclosing the achenes; receptacle areolate and glabrous or shortly fimbriate; corolla 7-18 mm long, the tube 1.4-5 mm long; achenes 2-6 mm long, erostrate, biform or (*C. patula*) the marginal ones merely obcompressed and unequally ribbed, in the other 3 species the marginal achenes paler, \pm compressed, the inner subterete; pappus white, 0.2-5 mm long. *Zacintha*, from *Zakynthos* or *Zante*, an island. Type species: *C. Zacintha* (L.) Bab.

Section 24.—*Phytodesia* sec. nov. Herba annua vel (*C. nicaeensis*) biennis; planta pubescens; radix tenuia vel crassa; caudex foliatus; folia infera oblanceolata petiolata dentata vel pinnatifida; folia supera similia vel sessilia reducta; capitula parva, parvissima vel (*C. nicaeensis*) media, 20-60-flora; corolla 5-11 mm longa, tubo 1.5-3 mm longo; achaenia 1.4-3.8 mm longa fusiformia erostrata vel rostrata 10-costata; pappus albus 1.5-5 mm longus.

Annual or (*C. nicaeensis*) biennial herbs; plant pubescent; root slender, ephemeral, or \pm woody; caudex leafy; caudical leaves oblanceolate, denticulate to pinnatifid, petiolate; cauline leaves similar or sessile and gradually reduced; stem erect, branched above or from near the base, or stems numerous, much branched from the base, many-headed; heads small or very small or (*C. nicaeensis*) medium, 20-60-flowered; outer involucre bracts $\frac{1}{4}$ - $\frac{1}{2}$ as long as the inner ones, or very small and linear; inner bracts glabrous on inner face, becoming carinate and spongy-thickened on outer face in fruit; receptacle areolate or alveolate, often finely ciliate; corolla 5-11 mm long, the tube 1.5-3 mm long; achenes golden, reddish, or very dark or pale brown, tawny or stramineous, 1.4-3.8 mm long, fusiform and beakless or with a very short coarse beak (in *C. parviflora* columnar) or with a fine beak $\frac{1}{4}$ - $\frac{1}{2}$ as long as the whole achene, 10-ribbed; pappus white, 1.5-5 mm long. *Phytodesia*, from *phyton*, a plant, + *desis*, a bond; referring to interconnecting relationships of the group. Type species: *C. nicaeensis* Balb.

Section 25.—*Lepidoseris* (Rehb., Fl. Exc. 1: 256. 1830-1832; et DC., Prod. 7: 153-154. 1838 excl. *C. alpina* L.). Perennial, biennial, or annual herbs; plant pubescent; root elongated, woody,

robust or slender; caudex leafy; caudical leaves rosulate, mostly oblanceolate, denticulate to pinnatifid, petiolate; cauline leaves similar or sessile and gradually reduced; stem or stems erect or decumbent, usually branched, few- or many-headed; heads large to small, mostly medium, 60-100-flowered; outer involucre bracts $\frac{1}{6}$ - $\frac{3}{4}$ (mostly $\frac{1}{4}$ - $\frac{1}{3}$) as long as the inner ones; inner bracts pubescent on inner face, becoming carinate or (*C. Clausonis*) convex on outer face, and spongy-thickened or (*C. Fontiana*) indurate; receptacle alveolate or areolate, ciliate; corolla 6-19 mm long, the tube about $\frac{1}{2}$ as long as the whole corolla; achenes various shades of brown, yellowish or greenish, uniform or (*C. Balliana* and some forms of *C. vesicaria*) bifid, 3-13 mm long, mostly fusiform and, at least the inner ones, definitely beaked, the beak ranging from very short to longer than the body, 10-ribbed; pappus white, dusky, or sordid white, or (*C. Claryi*) pale yellow, 3-6.5 mm long. Lepidoseris, from *lepis*, *lepidos*, a scale, + *seris*, endive or lettuce; probably referring to the prominent involucre bracts of the type species. Type species: *C. vesicaria* L.

Section 26.—**Nemauchenes** (Cass., Bull. Soc. Philom. 1818: 77; Diet. 34: 362. 1825 pro genus). Annual herbs; plant pubescent; root elongated, very slender to robust; caudex leafy; caudical leaves few or many, rosulate, lanceolate, oblong or oblanceolate, denticulate to pinnatifid; cauline leaves similar or sessile, gradually reduced or mostly bractlike; stem erect or stems semidecumbent, \pm branched, few- or many-headed; heads medium or small, 50-100-flowered; outer involucre bracts very short or $\frac{1}{4}$ - $\frac{1}{2}$ as long as the inner ones; inner bracts pubescent or (*C. juvenalis*) glabrous on inner face, becoming strongly carinate or navicular and spongy-thickened on outer face in fruit; receptacle alveolate or areolate, ciliate or (*C. aculeata*) glabrous; corolla 6-14 mm long, the tube 2-4.5 mm long; achenes dimorphic or (*C. aspera*, *C. setosa*) sometimes monomorphic, the marginal usually paler, compressed and beakless, the inner brown or tawny, fusiform and beaked, 10-ribbed or (*C. aculeata*) 16-18-ribbed; pappus white, 2.5-6 mm long. Nemauchenes, from *nema*, a thread, + *achanēs*, achene; referring to the finely beaked achenes. Type species: *C. aspera* L. = *N. aculeata* Cass., loc. cit.

Section 27.—**Psammoseris** (Boiss., Diag. Pl. Or. Nov. ser. 2, 11: 52. 1849 pro genus). Annual herbs; plant pubescent; root elongated, robust and woody, or slender and ephemeral; caudex leafy; caudical leaves rosulate, oblanceolate or elliptic, entire, dentate or pinnate; cauline leaves few, reduced or all bractlike; stems slender, mostly semidecumbent, few- or many-headed; heads small or (*C. Rueppellii*) sometimes medium, 20-60-flowered; outer involucre bracts $\frac{1}{4}$ - $\frac{1}{2}$ as long as the inner ones, linear or (*C. Rueppellii*) lanceolate; inner bracts pubescent or glabrous on inner face, becoming carinate and spongy-thickened in fruit; corolla 5-13 mm long, the tube 1.2-4 mm long; achenes brown, tawny, yellow, or stramineous, 3.5-7.5 mm long, fusiform (in *C. senecioides* also compressed), with a long fine or filiform beak (in *C. Rueppellii* the beak may be short and coarse), 10-ribbed or -striate (in *C. Rueppellii*, 10-15-ribbed); pappus white, 1.5-6 mm long. Psammoseris, from *psammos*, sand, + *seris*, endive or lettuce; referring to the desert habitat of the type species. Type species: *C. senecioides* Delile.

KEY TO THE SECTIONS

Countries or regions mentioned in this key are those in which the species are indigenous. Certain sections appear at more than one place in the key, and the species keyed out at a given place are designated by numbers.

A Caudex arising from a rhizome; rhizome horizontal, oblique or vertical, sometimes praemorse, rarely stoloniferous. (In *C. rhaetica* of sec. 4 the rhizome may be deeply penetrating in old plants, simulating a taproot.)

B Stems more or less branched, 3–30-headed or, if rarely 1–2-headed, then the stem at least 2 dm high and with 2–6 well-developed cauline leaves.

C Heads mostly larger and relatively wider; mature involucre 10–20 mm long, 4–15 (mostly 8–12) mm wide at middle; achenes 0.8–1.3 mm wide, coarsely ribbed or (*C. viscidula*) 25–35 striate.

D Plant tall, with a stout stem; cauline leaves remote, ascending.

E Caudical leaves coarsely dentate or runcinate-pinnatifid; achenes brown, pale brown, or stramineous, 20–35-ribbed or -striate (in *C. paludosa*, 10-ribbed), the ribs or striae narrow or unequal, with 3–5 stronger ones1. *Desiphylon*, p. 222

EE Caudical leaves finely denticulate; achenes very dark brown or black, 10–12-ribbed, the ribs very prominent.2. *Spathoides*, p. 238

DD Plant short, with slender stems; cauline leaves congested, spreading3. *Omalocline*, p. 241

CC Heads mostly smaller and relatively narrower; mature involucre 7–12 (mostly 8–11) mm long, 2.5–9 (mostly 3–5) mm wide at middle; achenes 0.3–0.8 (mostly 0.4–0.7) mm wide, finely ribbed or striate.

F Culine leaves several, the lower ones similar to the caudical leaves, the middle and upper one more or less reduced.5. *Mesomeris*, p. 273

FF Culine leaves few, all bractlike or reduced.

G Ligules 1.5–2 mm wide; anther tube 3–4.5 mm long; style branches 1–2 mm long; achenes 20-ribbed; pappus 2–4-seriate.13. *Intybellia*, p. 549

GG Ligules 0.6–1.2 mm wide; anther tube 1–2.4 mm long (in *C. Gmelini*, 4 mm long); style branches 0.4–1 mm long; achenes 10–12-ribbed; pappus 1-seriate21. *Microcephalum*, p. 721

BB Stems scapiform, 1-headed, sometimes 1-furcate, 2-headed, rarely 3-headed, usually low and leafless, never with more than 1 true leaf.4. *Brachypodes*, p. 248

AA Caudex arising from a taproot or from a subterranean shoot; root usually much elongated, sometimes short but then much wider than the stem or stems, sometimes forked, sometimes stoloniferous or generating adventitious buds from the lateral roots.

H Caudex strongly woody, in plants more than 1 year old covered with bases of old petioles or showing leaf scars; plants perennial or sometimes biennial.

I Receptacle with setiform paleae16. *Lagosotis*, p. 618

II Receptacle without setiform paleae.

J Caudical and lowest cauline leaves cataphyllous, appressed, scalelike18. *Pyrinachos*, p. 634

JJ Leaves not cataphyllous.

K Plants entirely glabrous or lightly tomentulose on the upper parts in 2 species; leaves small, spatulate or sessile, ovate, elliptic or obovate, mostly entire or denticulate, rarely lyrate and few-lobed, mostly glaucous or pergameneous12. *Ixeridopsis*, p. 530

KK Plants more or less pubescent; leaves larger, mostly oblanceolate, seldom glaucous or pergameneous.

L Plants with the basic chromosome number, $x = 11$. North America.15. *Psilochaenia*, p. 573

LL Plants with other chromosome numbers. Eurasia and Africa, not native in North America.

M Involucral bracts imbricate in anthesis; outer bracts conspicuously white-margined or pergameneous, becoming more or less differentiated from the inner bracts at maturity; achenes long-attenuate or long-beaked. 7. *Paleya*, p. 307

MM Involucral bracts not imbricate or if sometimes imbricate (*C. scaposa*, sec. 7), then the bracts not white-margined or pergameneous; outer bracts clearly differentiated from the inner ones in anthesis, if conspicuously white-margined (*C. heterotricha*, sec. 11), then the achenes columnar, not beaked.

N Aggregate inflorescence a narrow raceme; heads small, with 5-6 inner involucral bracts and 5-10 florets. S.E. Asia 17. *Napiseria*, p. 629

NN Aggregate inflorescence usually cymose, mostly corymbiform, sometimes scapiform or diffuse from the base of the stem, or if rarely racemiform, then much broader than in the preceding; heads larger, with more numerous involucral bracts and florets.

O Involucres at maturity strongly indurate, persistent, enclosing all the achenes; pappus very short, 0.2-0.4 mm long. Algeria 23. *Zacintha*, p. 742
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OO Involucres neither strongly indurate nor persistent, enclosing all the achenes; pappus much longer.

P Pappus setae very fine, only 2-4-celled in cross section at the base. Syria and near-by regions 19. *Phacasium*, p. 650
136

PP Pappus setae much coarser.

Q Achenes 13-20-ribbed or -striate (in *C. biennis*, sec. 10, with 10-20, but usually 13-18 ribs.)

R Involucres conspicuously hirsute, pilose or setose, with long dark hairs or setae, or if sometimes merely tomentose or glabrescent (*C. conyzaeifolia*), then the marginal florets 18-21 mm long and the inner involucral bracts not changed in fruiting heads 6. *Soyeria*, p. 295

RR Involucres not conspicuously hirsute, pilose or setose, or if densely villous (*C. vesicaria*, sec. 25, rarely), then the marginal florets only 7 mm long and the inner bracts carinate and thickened in fruit.

S Stems with 3-15 or more flower heads, or if only 1-2 headed, as in secondary stems or depauperate plants, then either the lower cauline leaves not bractlike, or (*C. auriculaeifolia*, *C. Raulini*) the caudical leaves regularly and saliently dentate, or (*C. oporinoides*) the achenes 7-10 mm long 10. *Berinia*, p. 421
59-71, 73, 75, 76,
78, 79, 84-87

SS Stems 1-headed, or if 2-headed or rarely 3-headed, then the cauline leaves bractlike, the caudical leaves not regularly and saliently dentate, and the achenes 4-6 mm long 11. *Macropodes*, p. 493
88-92, 95-101

QQ Achenes 10-12-ribbed or -striate (in *C. Rueppellii*, sec. 27, 10-15-ribbed).

T Caudical leaves dentate, denticulate or entire, or if rarely sub-pinnatifid (*C. alpestris*, *C. hypochaeridea*), then the involucres with some long black setae; involucres more or less setose, setulose, glandular or tomentose, never conspicuously spongy-thickened at the base; cauline leaves mostly bractlike, or if not mostly bractlike, then the involucres long-setose; branches strict except in *C. hypochaeridea brevicaulis*. Tropical and S. Africa; 1 species in Asia Minor and European Alps; 1 in S.E. Asia 8. *Anisorhamphus*, p. 330

TT Caudical leaves pinnatifid, or if dentate or denticulate, then the branches divaricate, or the involucre not conspicuously long-setose, or the cauline leaves not mostly bractlike, or the involucre spongy-thickened at the base. None of tropical Africa except Sec. 11, nos. 93, 94.

U Achenes beakless or very shortly beaked.

V Stems scapiform, 1-headed, or if furcate and 2-4-headed (*C. tenerrima*, *C. xylorrhiza*), then the pappus tawny 11. **Macropodes**, p. 493
93, 94, 96

VV Stems not scapiform, branched in various ways, and several- or many-headed; pappus white.

W Caudical leaves broadly spatulate, petiole long, narrow, blade ovate, coarsely retrorsely dentate, or if leaves oblanceolate and runcinate-pinnatifid, then the inner involucre bracts with a pale median dorsal stripe or nerve becoming yellow and carinate. W. Mediterranean reg. 9. **Gephyroides**, p. 405
56, 57

WW Leaves not broadly spatulate; inner involucre bracts without a pale median dorsal stripe or nerve.

X Achenes reddish or purplish-brown, yellowish at the apex. Siberia 14. **Mesophyllion**, p. 560
112, 113

XX Achenes not reddish or purplish-brown and yellowish at the apex. Mediterranean reg., Persia. 10. **Berinia**, p. 422
72, 74, 77, 80-83

UU Achenes, at least the inner ones, definitely beaked.

Y Stem or stems, at least the axis of each plant, erect from the caudex, or if sometimes arcuate or decumbent at the base, then erect above, mostly with several branches, never 1-furcate near the base; achenes always 10-ribbed and never with a beak longer than the body, except in *C. libyca*, which has a robust stem 25. **Lepidoseris**, p. 798
170-181

YY Stem or stems flexuous, arcuate or decumbent, mostly little stronger than the branches, or if sometimes with stems flexuous but nearly erect or much stronger than the branches, then (*C. bursifolia*) the achenes with a beak about twice as long as the body, or (*C. Rueppellii*) the achenes 10-15-ribbed, rather coarsely beaked. 27. **Psammoseris**, p. 892
190-193

HH Caudex not strongly woody; plants annual or biennial-monocarpic.

Z Receptacle with setiform paleae. 22. **Pterotheca**, p. 730

ZZ Receptacle without paleae, or if paleaceous (*C. fortida commutata*, sec. 20), then the paleae, flat, linear, awned.

a Pappus setae very fine, flexuous or straight, only 2-4-celled in cross section at the base; achenes dimorphic, beakless or (*C. pterothecoides*) often with a beak about $\frac{1}{2}$ as long as the achene. 19. **Phaeacasium**, p. 650
137-141

aa Pappus setae coarser, the larger ones more than 4-celled in cross section at the base; achenes bifiform or uniform, beakless or beaked.

b Achenes all beakless or (*C. neglecta*, sec. 24) sometimes with a very short coarse beak.

c Involucre in fruiting heads strongly urceolate; achenes characteristically bifiform, the diverse marginal achenes laterally compressed, ventrally winged or angled, these sometimes absent. 23. **Zacintha**, p. 743
157-159

cc Involucre in fruiting heads not strongly urceolate; achenes uniform.

d Achenes dark purplish-brown; receptacle ciliate. 14. **Mesophyllion**, p. 566
114

dd Achenes pale or golden brown, or if sometimes dark brown (*C. capillaris*), then not purplish, less attenuate; receptacle glabrous. 24. **Phytodesia**, p. 765
160-164

bb Achenes, at least the inner ones, definitely beaked (in *C. suberositis typica*, sec. 9, the beak very short).

e Inner achenes 7.5–21 (mostly 10–15) mm long; pappus completely extruded in mature heads 20. *Hostia*, p. 677

ee Inner achenes 2–9 (mostly 3–7) mm long; pappus not completely extruded.

f Achenes biform, the marginal beakless, paler in color, the inner beaked, or if achenes all beaked (*C. setosa typica* and forms of *C. aspera*), then the involucre setose, the setae strong or thick at the base. 26. *Nemauchenes*, p. 867

ff Achenes all beaked; involucre not strongly setose, sometimes finely setulose.

g Involucre mostly larger, 7–12 mm long, 4–8 mm wide; marginal florets 10–11 mm long; achenes shortly beaked, or if long-beaked, then the beak not over $\frac{2}{3}$ of the whole achene.

h Involucre gland-pubescent and black-setulose; style branches yellow; achenes 2.3–4 mm long, the beak from very short to $\frac{1}{4}$ of the whole achene. Algeria. 58
..... 9. *Gephyroides*, p. 411

hh Involucre gland-pubescent, not setulose, style branches green; achenes 6–8 mm long, the beak $\frac{1}{2}$ – $\frac{3}{4}$ of the whole achene. S. Russia, Caucasus, and Caspian regions 25. *Lepidoseris*, p. 863

gg Involucre mostly smaller, 3–8 mm long, or if sometimes 10 mm long (*C. senecioides*, sec. 27), then the beak of the achenes $\frac{3}{4}$ as long as the whole achene or longer; involucre 1.5–3.5 mm wide (in *C. apula*, sec. 24, sometimes 4 mm wide); marginal florets 6–8.5 mm long; achenes with short or long beaks.

i Achenes mostly shorter, 1.75–3.5 mm long, the beak short or never more than $\frac{1}{2}$ of the whole achene. N. Mediterranean littoral and Crete. 182
..... 24. *Phytodesia*, p. 765

ii Achenes mostly longer, 3.5–7.5 mm long, the beak, at least on the inner achenes, $\frac{1}{2}$ – $\frac{3}{4}$ as long as the whole achene, or longer. S. Mediterranean littoral. 165–169
..... 27. *Psammoseris*, p. 892

SECTION 1. DESIPHYLION

Relationships of the Species

The 4 species of this section are characterized by a strong rhizome, a robust stem, large coarsely petiolate lower leaves, and gradually reduced upper leaves, few branches, most of which arise above the middle, heads with many florets and numerous involucre bracts, the longest outer bracts $\frac{1}{4}$ – $\frac{2}{3}$ as long as the inner, and the inner bracts little changed at maturity. All but *C. paludosa* are further characterized by stout peduncles which become inflated toward the head, large-sized heads, large florets, and large achenes, with multiseriate coarse pappus bristles. The peculiarities of *C. paludosa* are discussed below. Of the other 3 species, *C. sibirica* is definitely the most primitive morphologically. It has the largest and most promi-

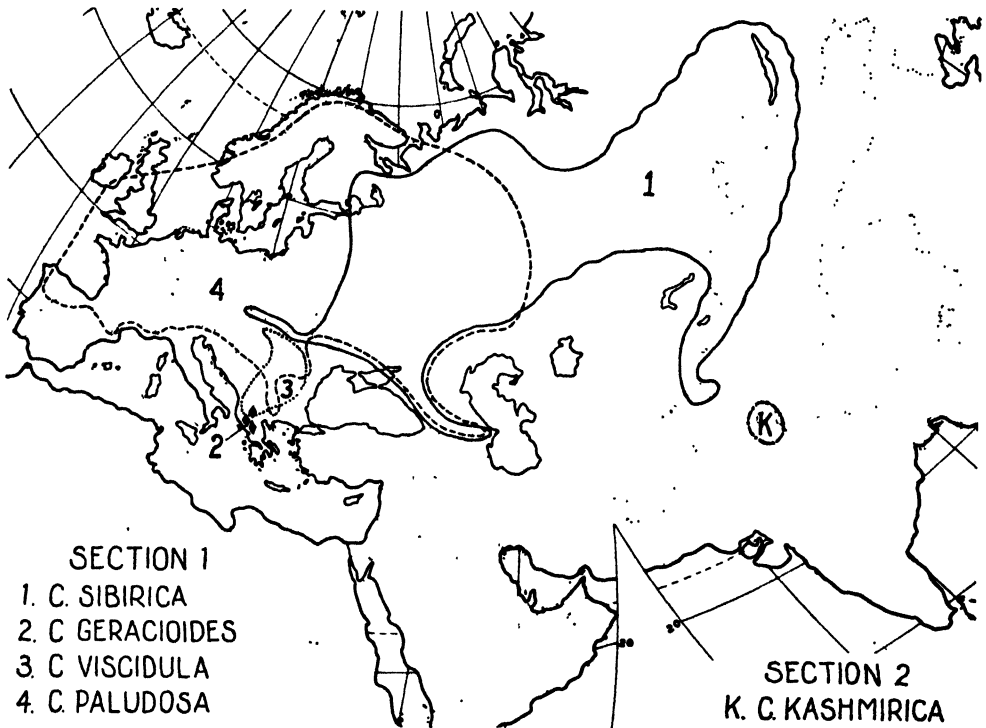


Fig. 12. Geographic distribution of the 4 species in sec. 1 and the 1 species in sec. 2. Note the overlapping ranges of the widespread species, *C. sibirica* and *C. paludosa*, in contrast with the endemic *C. kashmirica* and *C. geracioides*. The 3 known stations for the latter are indicated by diamonds. Based on Goode Base Map No. 201 PC. By permission of the University of Chicago Press.

nently ribbed achenes, with the longest and coarsest pappus; it also has the most numerous and broadest outer involucre bracts, which are somewhat imbricate. Next in order on the basis of these features are *C. geracioides* and *C. viscidula*. But these 2 species have 6 pairs of chromosomes, whereas *C. sibirica* has 5 pairs. Furthermore, the chromosomes of *C. geracioides* are somewhat more symmetrical than those of *C. sibirica* (figs. 13, 14). Thus, the morphologic and karyotypic criteria are not in agreement for these species. But such discrepancies are not surprising, since we are dealing here with just a few remaining "twigs" on the generic "tree." The immediate ancestors of all 4 species seem to have become extinct.

As indicated above, *C. paludosa* stands apart from the other 3 species in that it

is more reduced in size of peduncles, heads, florets, and fruits; also, the achenes and pappus have certain resemblances to those of many *Hieracium* species. But the chromosomes are quite similar to those of *C. viscidula*. The possible significance of these peculiarities is discussed under *C. paludosa*.

There is sufficient resemblance between these 4 species to warrant the assumption that they descended from the same ancestral line, with the possible addition of a *Hieracium*-like ancestor for *C. paludosa* through hybridization. Indeed, it is conceivable that all 4 species arose through hybridization between certain closely related 6-paired species. But it is equally conceivable that the 5-paired karyotype of *C. sibirica* originated through structural changes in the chromosomes of just one of those 6-paired ancestral species. That the ancestors of these species bore greater similarity to the primitive genus *Dubyaea*, with respect to both morphology and chromosomes, is a reasonable assumption.

The distribution of these 4 species (see fig. 12) is significant for any hypothesis concerning the center of origin of the genus. *C. sibirica* is a widespread species, its range extending from Transbaikalia in E. Asia to the Carpathian Mts. in E. Europe, and from the Pamir reg. in S. Central Asia almost to the Arctic Circle in N. Russia. Obviously, it is adapted to a cold-temperate climate and, from its present distribution, it may logically be assumed to have originated in the Altai reg. of N. Central Asia. *C. geracioides* is a restricted endemic of the S. Balkan Pen., and it occurs at low montane stations in association with the common beech. Just as obviously, it is a warm-temperate plant and, if it originated in Central Asia, was presumably at a lower elevation than *C. sibirica* or in a more southerly part of the region or both. Under these conditions it could have migrated to its present location by way of a southerly route through Iran and Asia Minor. *C. viscidula* occurs in the N. Balkan Pen.; but in the E. Carpathian Mts. it is associated with the Dacic or southern element, and hence it also probably migrated from Central Asia by a southern route. From the present widespread distribution in Europe of *C. paludosa*, if it also originated in Central Asia, it is most logical to assume that it reached its present area by way of a route over or around the southern end of the Ural Mts., before Pleistocene time. That many species of plants migrated into Europe by way of both a southwesterly and a northwesterly route from Central Asia is certain, evidence for this statement having been reviewed in chapter 6 of Part I. Here it is sufficient to point out that in the distributions of these species we find the guideposts to the principal routes of migration which appear to have been followed by many species of *Crepis* from the assumed center of origin in N. Central Asia.

Key to the Species of Section 1

- Longest outer involucre bracts $\frac{1}{2}$ – $\frac{2}{3}$ as long as the inner; corolla tube sparsely pubescent, with 2- or many-celled trichomes; filaments of the anthers equal or nearly so.
 - Caudical and lower cauline leaves spatulate, the blade often cordate at the base, petiole broadly alate, often as long as the blade; involucre 15–20 mm long, 10–15 mm wide, hairy, tomentose or glabrous; corolla 20–30 mm long; achenes 8.5–11 mm long; pappus 9–10 mm long 1. *C. sibirica*, p. 223
 - Caudical and lower cauline leaves deeply runcinate-pinnatifid, gradually attenuate toward the base, petiole narrowly alate, $\frac{1}{4}$ – $\frac{1}{3}$ as long as the blade; involucre 11–13 mm long, 5–8 mm wide, densely setose; corolla 16–18 mm long; achenes 5.5–6.5 mm long; pappus 7–8 mm long 2. *C. geracioides*, p. 226
- Longest outer involucre bracts $\frac{1}{4}$ – $\frac{1}{3}$ as long as the inner; corolla tube densely pubescent, with very short fine hairs or glabrous; filaments of the anthers very unequal.
 - Peduncles stout, inflated at maturity; involucre 11–13 mm long, about 8 mm wide at middle in fruit; corolla about 21 mm long, the tube finely pubescent; achenes gradually attenuate toward the apex, 25–35-striate; pappus white 3. *C. viscidula*, p. 229

Peduncles slender, not inflated at maturity; involucre in largest heads 10–12 mm long, 4–6 mm wide; corolla 13–17 mm long, the tube glabrous or with a few very short hairs near the base; achenes columnar, 10-ribbed; pappus yellowish 4. *C. paludosa*, p. 232

1. *Crepis sibirica* L.

Sp. Pl. 807. 1753. (Fig. 13.)

Perennial, 3–15 dm high; rhizome woody, bearing strong fibers, crowned with the narrow woody caudex bearing the monocarpic stem; early caudical leaves disappearing in nature; later caudical and lower cauline leaves 10–40 cm long, 4–9 cm wide, ovate or oblong, acute, petiolate, the blade often cordate at base, sinuous-dentate, rugose, pubescent on lower face, with pale glandless hairs especially on veins, puberulent or glabrescent on upper face, the petiole often as long as the blade, strongly alate and dentate, amplexicaul at base; upper cauline leaves ovate, oblong or lanceolate, acute, sessile, amplexicaul, dentate, denticulate or entire; stem erect or sinuate, 4–8 mm wide at base, terete, striate or strongly sulcate, \pm tomentose and setose, cymosely branched near summit, branches strict or divaricate, 1–4-headed; peduncles stout, 1–15 cm long, straight or arcuate, tomentose, \pm setulose; heads erect, large, many-flowered; involucre campanulate, 15–20 mm high, 10–15 mm wide at middle in fruit, \pm pubescent, with dark or pale green glandless hairs or puberulent, tomentulose or glabrous; outer bracts 12–18, \pm imbricate, unequal, longest $\frac{1}{2}$ – $\frac{2}{3}$ as long as the inner, 3–4 mm wide, outermost deltoid or ovate, innermost oblong or lanceolate, acute, strongly ciliate at margin near the apex; inner bracts 12–16, oblong or lanceolate, acute, strongly ciliate near the apex, glabrous on inner face, scarcely changed at maturity, ultimately reflexed; receptacle convex, 6–8 mm wide, areolate-fimbriate, areoles whitish, interspaces brownish, fimbriae shortly ciliate; corolla in marginal florets 20–30 mm long, 2–2.5 mm wide; teeth 0.5–1 mm long; corolla tube 7–9 mm long, densely or sparsely pubescent, with coarse many-celled trichomes 0.1–1 mm long; anther tube (5)6 \times 1.5 mm dis.; appendages 0.7–0.8 mm long, oblong, truncate, obtuse or acute; filaments 1–1.5 mm longer; style branches 2.5–3.5 mm long, 0.2 mm wide, attenuate at tip, yellow or greenish; achenes brown, 8.5–11 mm long, 1–1.3 mm wide, straight or curved, fusiform, terete or the marginal somewhat obcompressed, \pm attenuate at the paler summit, with expanded pappus disk, narrowed at the strongly calloused closed base, about 20-ribbed, ribs fine, rounded, smooth or muriculate under lens, with 3 of the ventral and sometimes 1 of the dorsal ribs stronger than the rest; pappus yellowish-white, 9–10 mm long, 3-seriate, the setae unequal in length and width, the coarsest 50–80 μ wide at base, densely barbellulate, strongly persistent. Flowering June–Aug.; flowers yellow. Chromosomes, $2n = 10$.

Hieracium sibiricum Lamk., Encycl. Méth. 2: 368. 1786.

Sonchus flexuosus Ledeb., Hort. Dorpat. Suppl. 1: 5. 1806–1810.

Sonchus caucasicus Biehl., Cent. Pl. Rar. 12. 1807 et Spreng., Fl. Hal. Mant. 1: 49. 1807.

Soyeria sibirica Monn., Ess. Hierac. 77. 1829.

Aracium sibiricum Sch. Bip., ex Herd., Bull. Soc. Nat. Mosc. 43: 213. 1870.

Hieraciodes sibiricum O. Kuntze, Gen. 1: 346. 1891.

E. Europe: At a few widely scattered stations in the Carpathian Mts., and one in the Gesenke Mts., a northwestern extension of the same system; Podolia (W. Ukraine), and thence throughout Russia; more definitely from N. Armenia (acc. to Ledebour [R] 2: 828) to E. Finland, Archangelsk, the Petschora R. valley, Samojed Land, and the middle Ural Mts. Asia: From the Urals to Transbaikalia and southwestward in the mountains of W. Mongolia and E. Turkestan (to the Alai-Pamir region, acc. to Fedtschenko, 205).

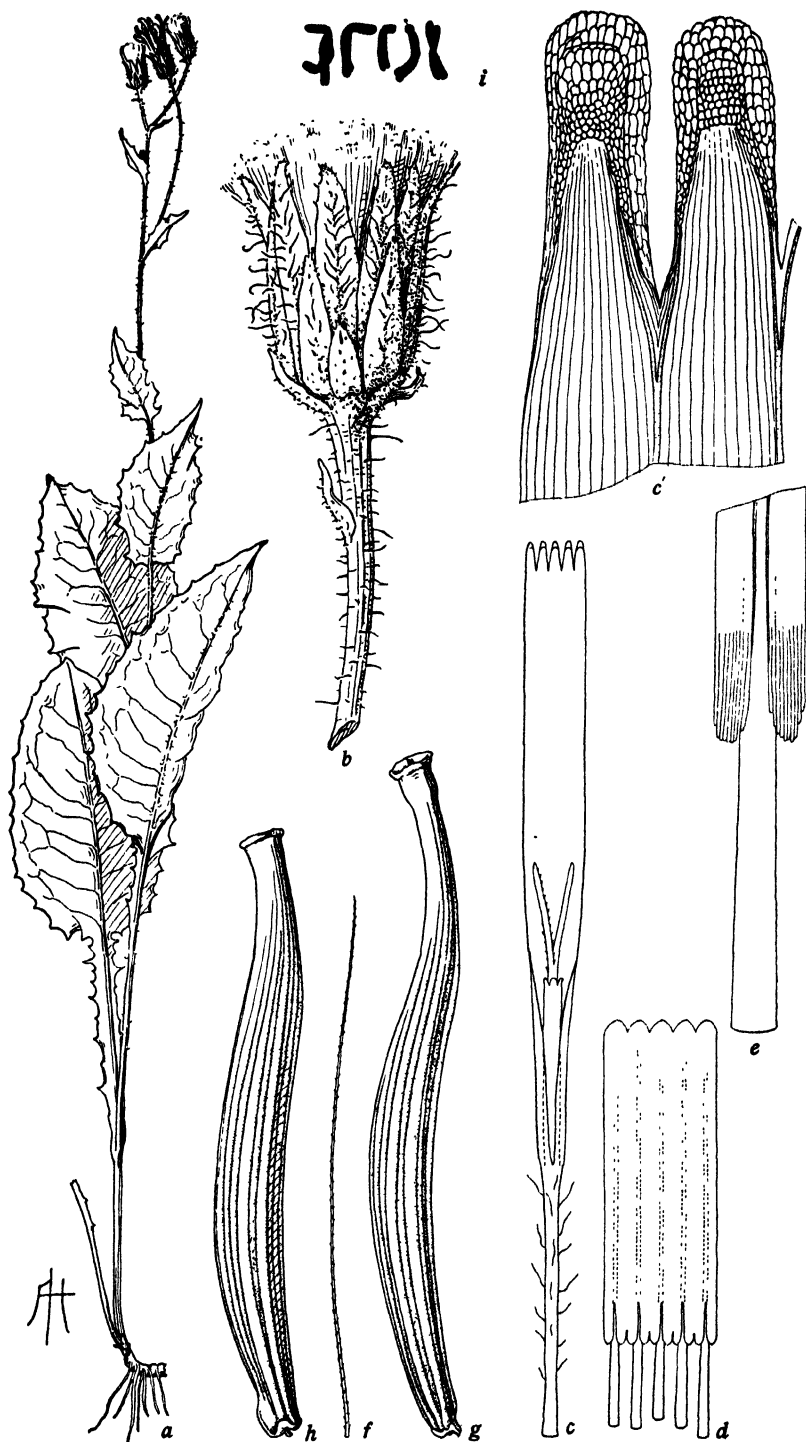


Fig. 13. *Crepis sibirica*, *a-f*, from Lindroth et Cajander in 1898 (UC 250678); *g, h*, from hort. genet. Calif. 30.2765 (UC 620570); *i*, from hort. genet. Calif. 1862: *a*, plant, $\times \frac{1}{4}$; *b*, head, $\times 2$; *c*, floret lacking ovary, $\times 4$; *c'*, detail of ligule teeth, $\times 50$; *d*, anther tube, $\times 8$; *e*, detail of appendages, $\times 32$; *f-h*, pappus seta and achenes, $\times 8$; *i*, somatic chromosomes, $n = 5$, $\times 1250$.

Crepis sibirica is listed by Pax (1: 226) as 1 of 6 species of flowering plants comprising a typical "Siberian" element of the Carpathian flora. Like *Actaea Cimicifuga*, another member of this sextet, *C. sibirica* finds its southwestern limit in the Carpathian system. Acc. to Hegi (1138), this species no longer exists in the Sudeten Mts., and he questions whether it still can be found in the "Grossen Kessel" in the Gesenke Mts. At a former station in the Malenitza Mts., in Hungary, it has been extinct for more than a century. Two collections purporting to have come from the Alps are refused recognition because of insufficient evidence. Acc. to Pax (*op. cit.*, 2: 148), in the W. Carpathians, *C. sibirica* occurs in an area characterized by numerous old relic species; but, like *Primula acaulis* and *Senecio umbrosus*, from its distribution and associations it appears to have a higher heat requirement than most of those relics. Acc. to Hegi (*loc. cit.*), it is found in forests of oak and linden in Podolia (Ukraine); whereas in Russia and Siberia it behaves as a steppe plant.

In view of its wide geographic distribution, as well as its most primitive position in the genus, it is not surprising that this species exhibits considerable variation in gross morphology. This tendency is emphasized by the study of garden cultures grown from seed obtained from wild plants in widely separated localities. In general, however, the variations observed by the writer in such geographic races were of minor importance. Only two notable departures from what may be considered the norm for the species were encountered. In one accession from an unknown locality in Mongolia (hort. genet. Calif. 2764) all the plants were dwarf in stature and they bloomed about 2 months earlier than the other accessions. Similar dwarf plants appeared in an accession from the Leningrad Botanic Garden (hort. genet. Calif. 2787). It may well be that these striking differences in stature and time of flowering have a simple genetic basis. At any rate, these differences do not seem to be correlated with other notable variations. The other race showing a major departure from the norm of the species was an accession received from the Belgrade Botanic Garden (hort. genet. Calif. 1997, original source unknown). These plants were unusually vigorous and robust, but, except in their achenes, which were only 7 mm long and purplish-brown in color, were otherwise typical. They were also constricted rather than attenuate at the summit, and some of the marginal achenes were definitely obcompressed with fairly strong lateral and median ribs. This type of achene is reminiscent of *Youngia*, and its occurrence in one strain of this primitive species of *Crepis* may have some phylogenetic significance.

Czechoslovakia: Gesenke Mts., "Kessel," slopes, *Lans* in 1909 (UC); *ibid.*, Grossen Kessel, *Oborný* in 1876 and 1877 (Bur, K); Fatra Mts., Mt. Revan, near Gajdel, dolomitic soil, *Pantocsek* 2018 in 1883 (Bur, Mo, Minn); Sudeten, Fessel (Kessel ?) Valley, *Winckler* in 1874 (Bur); Silesia, Mt. Alvater, *Niesel* in 1862 (Bur). **Russia:** Leningrad dist., near Roparje (*anonymous*), 362B (K); Karelia Prov., Olonets dist., near headwaters of the Svir R., *Lindroth* and *Cajander* in 1898 (UC, Mo); Archangel Prov., ex hort. genet. Calif. 30.2765 (UC); Moscow, *Demidoffe* in 1785 (Ms); Kaluga Prov., *Minkvoitz* (UC); Minsk (?) Prov., Tala (= Tal or Talka ?), *Zinger* in 1923 (Bur); Orel Prov., near Palna, *Gruner* in 1868 (K); Tambow Prov., *Schirajewsky* in 1900 (Bur); Saratov reg., ex hort. genet. Calif. 29.2444 (UC). **Siberia:** without locality or collector (L) type; Altai, southern, Kandagatai, *Potanin* in 1876 (NY); Altai, villages of Arachabasch and Kebezeny, *Schischokin et al.* in 1931 (NY); near Toms, in a meadow with trees, *Sergievskaya* in 1927 (NY); Jenisseisk Prov., Krasnojarsk and Atschinsk, *Kusnezow* in 1912 (UC); Irkutsk Prov., Oka-Angara R. reg., *Krystofovic* in 1910 (UC); Transbaikalian reg., Onon R. basin, *Ikonnikov-Galitzky* in 1928 (UC). **Mongolia:** Dzungaria, Tarbagatai reg., *Ledebour* misit in 1844 (Mo); Samdalita R., a tributary of the Zacharin R., edge of a birch forest, *Ikonnikov-Galitzky* in 1929 (UC); locality ?, ex hort. genet. Calif. 30.2764 (UC); locality ?, ex hort. genet. Calif. 30.2787, cult. from seeds received from Hort. Bot. Petrop. (UC); E. Kentei Mts., source of Kerulen R. and Onon R., road to Mt. Khudjirian, deciduous forest, *Ikonnikov-Galitzky* 1846 (NY). **Tien Shan:** *Massegetov* and *Massalsky* in 1925 (NY).

Relationship

Crepis sibirica and *C. geracioides* are the most primitive species in the genus, since they show near affinity with the most primitive Cichoriaceous genus *Dubyaea* in habit, leaf shape, involucre, and achenes. Unlike *C. geracioides* and *C. viscidula*, *C. sibirica* has a wide geographic distribution, and it is variable in stature, in season of maturity, and in size, shape, and color of the fruits. It is not unlikely that a thorough study of the genetics and distribution of *C. sibirica* will reveal the existence of subspecies. Morphologically, because of its larger heads, florets, and fruits, this species is more primitive than *C. geracioides*, and the fruits in some forms of *C. sibirica* resemble those of *Dubyaea* more closely than do the fruits of *C. geracioides*, whereas in another form they resemble the achenes of primitive *Youngia* types. But the fact that *C. sibirica* has only 5 pairs of chromosomes, against the 6 found in *C. geracioides*, indicates that the reduction in number of chromosomes from 12 to 10 occurred very early in the history of the genus. Furthermore, it seems probable that this important change in chromosome number was associated in some way with the events which produced the morphologically peculiar chromosomes of *C. pygmaea* and all the species of sec. 5. The morphology of the plants shows that these 3 sections are closely related; and it seems highly probable that they originated in a common development center. But whether they all had a similar early migrational history is another question.

The present distribution of *C. sibirica* can be interpreted in terms of either of two migrational histories starting at an assumed center of origin in N. Central Asia, from which its present distribution in Siberia and Turkestan-Mongolia would naturally follow: (1) It may have moved southward and westward in late Oligocene or early Miocene times through E. Turkestan, Iran, N. Asia Minor and the Balkan Pen. to reach approximately its present distribution in the mountains of E. Europe. (2) Or it may have migrated into Europe from N.W. Asia over the S. Ural reg. after the closing of the Obic Sea in early Miocene. It could then have spread westward and southwestward in Europe, reaching refugial areas, during the maximum southward glacial advance. From these refugial areas it could have followed the retreating ice northward, establishing its present distribution while also occupying its present limited areas in the Carpathian mountain system.

In view of the wide and far northern distribution of both *C. sibirica* and *C. paludosa* at present, the second hypothetical migration history, with respect to these 2 species, seems more logical than the first.

2. *Crepis geracioides* Hausskn.

Ex Nym., Consp. Fl. Eur. Suppl. II. 1: 201. 1889; Mitth. Thür. Bot.
Ver. N. Folge. 7: 52. 1895. (Fig. 14.)

Perennial, 3.5–7.5 dm high; rhizome oblique, bearing many long fleshy fibers; caudical leaves 4–6, up to 24 cm long, 6 cm wide, obovate to oblanceolate, acute or obtuse, gradually attenuate into a narrow winged petiole $\frac{1}{4}$ – $\frac{1}{3}$ as long as the blade, deeply runcinate-pinnatifid or sublyrate, finely and shortly ciliate on margin, pubescent on veins beneath, with yellow glandless hairs, similarly pubescent above, becoming glabrescent; lower cauline leaves similar but sessile or panduriform, amplexicaul or subamplexicaul, acuminate, upper cauline leaves lanceolate or linear, entire, or bractlike; stem erect, terete, fistulose, striate, densely pubescent near base, glabrous above, simple and 1-headed or 2–4-branched, branches pedunculate; peduncles erect or sinuate, 10–35 cm long, stout, terete, fistulose, inflated near head but constricted just below the head, like involucre canescent-tomentulose or farinose; heads erect, large, about 60-flowered; involucre campanulate, 11–13

mm high, 5–8 mm wide at receptacle; outer bracts 10–12, unequal, outermost very short, longest $\frac{1}{2}$ – $\frac{2}{3}$ as long as inner bracts, lanceolate, acute, like inner bracts, canescent-tomentulose or farinose, densely setose with long green glandless bristles and finely pubescent with appressed hairs; inner bracts 14–18, in 2 series, the inner ones slightly longer and little setose, lanceolate, acute or acuminate, white-ciliate at the apex, ventrally glabrous and strongly nerved, little changed at maturity; receptacle areolate, glabrous; corolla 16–18 mm long; ligule 2–3 mm wide; teeth 0.3–0.8 mm long; corolla tube 4–6 mm long, sparsely beset with short (0.2–0.4 mm long), 2-celled trichomes, sometimes with a few coarse several-celled tortuous hairs near the summit; anther tube (4) 4.5×1.25 (2) mm dis.; appendages 0.6–0.8 mm long, each appendage distinctly 2-parted, upper part sagittate, lower part oblong, obtuse, or acute, and usually with a short apical claw; filaments 1.3–2 mm longer; style branches 2 mm long, 0.2 wide at base, gradually attenuate to the acute tip; achenes pale brown when mature, 5.5–6.5 mm long, 1 mm wide, the marginal strongly curved near base and dorsoventrally compressed, the inner ones nearly straight and subterete or irregularly angular, slightly but definitely attenuate to the apex, without an expanded pappus disk, narrowed at the strongly calloused base, about 30-striate, striae narrow, nearly equal or sometimes with 4 or 5 definitely stronger ones, very finely spiculate under lens and often with a few fine white cilia near the apex; pappus white, 7–8 mm long, 2-seriate, rather coarse (50 – 65μ wide at the base), stiff, united at base, and coming away in sections, persistent, exceeding the involucre. Flowering June–July; flowers deep chrome-yellow; anther tube yellow, with 5 reddish-brown nerves; style branches yellow. Chromosomes, $2n = 12$.

Greece: In subhumid places on Mt. Zygos on siliceous serpentine substratum; and, acc. to F. Markgraf (*in litt.* et in Hayek, *Prod. Fl. Penin. Balc.* 2[5] no. 3364. 1931), in Albania on Mt. Gur-i-Topit, southwest of Lake Ochrid, in a beech forest on serpentine at 1700 m alt. Markgraf also cites Hayek as authority for its occurrence in Macedonia. The specimens cited first below were collected later than the publication of the original description, which cites no particular specimen. The type, collected by Haussknecht, has not been seen by the present author, but the original description is full and precise, and there is no mistaking the identity of this distinctive species.

Monomorphic.

Greece: N.W. Thessaly, Pindus Tymphaeus Mts., among beeches (*Fagus* sp.) on Mt. Zygos, *Sintenis* 912 (K, B, Bur); Pindus Mts., Zygos, above Malakasi, *Miss S. P. Topali* 1, 11, 12 (UC).

Relationship

This monomorphic species, in its morphological characteristics, is certainly closer to *C. sibirica* than to any other species, although the two differ in many details. Its achenes are closely similar to those of *C. sibirica* and the pappus is similar except that it is nearly white and not quite so coarse and stiff as in *C. sibirica*. The two species are also similar in the rhizomatous subcaudex and the habit of the plant, but the leaves of *C. geracioides* are intermediate between those of *C. sibirica* and *C. lapsanoides*. In shape of the involucre and involucral bracts both *C. geracioides* and *C. viscidula* are more like *C. lapsanoides*. Thus, *C. geracioides* and *C. viscidula* appear to be connecting species between *C. sibirica* and the species of sec. 5. But Haussknecht's classification of *C. geracioides* in "Eucrepis" was entirely unjustified, because its setaceous involucre is merely indurate and otherwise little changed in mature fruiting heads.

Although the 6 pairs of chromosomes of *C. geracioides* exhibit a higher degree



Fig. 14. *Crepis geracioides*, a, b, and h, from Sintenis 912 (B, K); c-g and i, from Topali 12 (UC 655336): a, plant, $\times \frac{1}{2}$; b, head, $\times 2$; c, floret, $\times 4$; c', trichome from corolla tube, $\times 100$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, g, 2 achenes, each with a pappus seta, $\times 8$; h, h', 2 inner involucre bracts, outer and inner faces, respectively, $\times 4$; i, somatic chromosomes, $n = 6$, $\times 1250$.

of asymmetry than those of *C. kashmirica*, which comprises sec. 2, yet the many morphological resemblances of *C. geracioides* to *C. sibirica*, and of both these to *Dubyaea*, justify the classification of *C. geracioides* in sec. 1 rather than in sec. 5.

Comparing the karyotype of *C. geracioides* with those of *C. lapsanoides* and *C. sibirica* (see figs. 13, 14, 33) reveals striking similarities to both and suggests that *C. geracioides* may represent an ancestral stock from which at least some of the *Mesomeris* species were derived. Its chromosomes are mostly strongly asymmetrical, but they do not have the unusually peculiar features found in the *Mesomeris* species. Whether *C. geracioides* itself was of hybrid origin or whether it hybridized with other 6-paired species to produce the remarkable series of types found in sec. 5 can only be conjectured. In line with the idea that *C. geracioides* was of hybrid origin is the fact that its pollen is very irregular in size, ranging from 28 to 43 μ ; although large-sized grains predominate, the average of 20 grains is 36 μ .

The very local distribution of this species and its apparent restriction to a serpentine substrate characterizes it as a relic type. In order to have produced the widely distributed members of sec. 5, *C. geracioides* itself must of necessity have been widely distributed in earlier times. All of the known stations for this species are in N. Greece or closely adjacent districts. This limited, extremely southern distribution strongly indicates that *C. geracioides*, like *C. pygmaea* and the species of sec. 5, followed the Turano-Irano-Pontic migration route from N. Central Asia. With such a migration it could easily have been involved in the development of species of sec. 5.

3. *Crepis viscidula* Froel.

Ex DC., Prod. 7: 166. 1838. (Fig. 15.)

Perennial, 2.5–6 dm high; rhizome horizontal, slender, woody, strongly fibrillate; caudical leaves few, disappearing early, up to 17 cm long, 5 cm wide, the blade elliptic, acute, coarsely retrorsely dentate, or lyrate, with the terminal lobe large, hastate, the lateral lobes few, small, attenuate into a short- or long-winged petiole, glabrous, glabrescent or pubescent, with fine pale glandless hairs; lowest cauline leaves similar, the others oblanceolate, lanceolate or ovate, acuminate, acuminate-dentate or denticulate, sessile, rounded-amplexicaul, gradually reduced upward, only the very uppermost bractlike; stem erect, sinuate, terete, striate, pubescent, with or without glands, or glabrous, cymosely 1–5-branched near the top, the branches pedunculate, forming an open corymbiform inflorescence, or paniculately branched from the middle, the lower branches short or elongated, 1–2-headed; peduncles stout, 2–16 cm long, striate, gradually thickened toward the head, 1–3-bracteate, lightly tomentulose and gland-pubescent, with short or long fine black or greenish hairs; heads erect, medium, 30–60-flowered; involucre campanulate, 11–13 mm high, about 8 mm wide at middle in fruit, dark green, finely tomentulose, densely pubescent, with short and long hairs bearing pale or brown glands; outer bracts 10–15, very unequal, the longest $\frac{1}{4}$ – $\frac{1}{2}$ as long as the inner, narrowly deltoid to linear; inner bracts 14–21, lance-linear, acuminate, glabrous on inner face, little changed in young fruiting heads, but at full maturity becoming convex dorsally, unchanged in color, but definitely spongy-thickened near the base, ultimately reflexed; receptacle areolate, glabrous; corolla about 21 mm long; ligule 2.25 mm wide; teeth 0.4 mm long; corolla tube about 4.5 mm long, beset with very short (0.05–0.1 mm long) stout-pointed trichomes; anther tube about 5.75 \times 1.2 mm dis.; appendages 0.8 mm long, oblong, acute or obtuse; filaments unequal, 0.7–1.8 mm longer; style branches about 2.5 mm long, 0.1 mm wide, acute, yellow; achenes light brown or brown, 5.5–8.5 mm long, 0.7–1 mm wide, the marginal somewhat obcompressed, fusiform and abruptly attenuate to both ends,



Fig. 15. *Crepis viscidula*, a-d, from Pančić in 1869 † (Bo); e-k, from Stefanoff in 1929 (UC 470086-7): a, plant, $\times \frac{1}{4}$; b, floret lacking ovary, $\times 4$; c, anther tube, $\times 8$; d, detail of appendages, $\times 32$; e, lower part of a plant showing branching rhizome and bases of old stems, $\times \frac{1}{2}$; f, old head, $\times 2$; g, 3 inner bracts and 1 outer one, outer face, $\times 4$; h-j, 2 achenes and a pappus seta, $\times 8$; k, somatic chromosomes, $n = 6$, $\times 1250$.

or columnar and gradually attenuate upward, 0.4–0.6 mm wide below the slightly expanded white pappus disk, constricted at the lightly calloused small hollow base, 25–35-striate, striae nearly equal, close, narrow, rounded, smooth, sometimes with 3 stronger ones on ventral face in marginal achenes; pappus white, about 6 mm long, 2–3-seriate, setae very unequal in length and width, outermost shorter and finer, the coarsest about 50μ (6 cells) wide, rather soft but somewhat brittle, persistent. Flowering July–Aug.; flowers yellow. Chromosomes, $2n = 12$.

Hieracium pyrenaicum Roch., Pl. Banat. Rar. 69, t. 29, f. 59. 1828, non L.

H. ochroleucum Panč., ex Nym., Consp. 455. 1878–1882, non Schleich.

Soyeria serbica Sch. Bip., Pollichia 22–24: 322. 1866.

Crepis serbica Panč., ex Boiss., Fl. Orient. 3: 843. 1875.

C. nigra Velen., Act. Soc. Sci. Bohem. 1887: 28, ex Nym., Consp. Suppl. 2: 201. 1889.

Hieraciodes viscidulum O. Kuntze, Gen. 1: 346. 1891.

Mountains of Hungary, Rumania, Bulgaria, Bosnia, Hercegovina, Montenegro, Serbia, and Albania. Moist places in meadows and among trees mostly in subalpine locations from 1100 to 2300 m alt.

This species is monomorphic, allowing for minor variations in size, amount of pubescence, etc. Although the type has not been seen by the present author (there was no specimen in Herb. DC. Prod.), the identity of specimens cited below, with *C. viscidula* Froel., has been certified by Stefanoff (*in litt.*, 1927) and Markgraf (*in litt.*, 1932), as well as by Pančic (Fl. Prin. Serb. 463. 1874) and Velenovsky (384).

Although specimens from Rumania have not been seen by me, Javorka and Csapody (Magy. Fl. Kepek. 566. 1934) report this species from "high elevations in the Carpathians, Transylvania." Acc. to Pax (1: 231; 2: 252), this species is classified as of the Dacic element (Dacia = Transylvania), which extends from Siebenbürgen into the N. Balkan Pen. The plant occurs in subalpine meadows in the Rodnaer Alps, the Burzenland Mts., and the Transylvanian Alps with other characteristic Dacic types. In the Bihar Mts. it occurs in a mixed flora of various elements. *C. viscidula*, acc. to Stefanoff (*in litt.*), occurs locally in 7 small areas in the western half of Bulgaria, on meadowy slopes and in open places in the forest up to 2300 m alt. Adamovic (252) reports it from submontane oak woods in the Balkan Pen. Acc. to Bornmüller (Engler Bot. Jahrb. 60 [3]: 121. 1926), it occurs in S. Serbia as a very rare plant on Mt. Perister at 1800 m among *Pinus Peuce*. This pine, acc. to Schwarz (214), is a characteristic species of the Mediterranean reg., considering this term in the widest sense; and it is allied with an Afghano-Sindian element which must have followed the Pontic-Iranian migration route into the Balkan Pen. in early Tertiary time. Although the association of *C. viscidula* with this pine on Mt. Perister may be merely coincidental, it reminds one that the present distribution of secs. 3 and 5 is sufficient in itself to indicate very definitely that most of these species, like *C. viscidula* and *C. geracioides* of sec. 1, were derived from a Central Asiatic source and reached their present locations by way of an Iranian-Pontic-Balkan route.

Hungary: Mt. Verfu Pelaga, Betyezat, in 1903 (Bur); Biharia, Kerner (UWG). **Bulgaria:** Na Vitoši, Velenovsky in 1885 (PV) as *C. nigra*; Mt. Bogoveka planina, Velenovsky in 1887 (PV); Mara-gidik, Urumoff in 1897 (UWH); Mt. Pirin, Suchadal Valley, calcareous soil, 1200–1800 m, Georgieff in 1932 (UC); Mt. Vitoscha, alpine meadows, 2000 m, Stefanoff in 1929 (UC); Rhodope Mts., Strybrny in 1897 (K). **Serbia:** south-central, stony place among trees, Pančic in 1869 ? (Bo) as *Soyeria serbica*; Niš, subalpine, calcareous soil, Adamovic in 1894 (Mu); Basara, among trees, subalpine, 1100 m, Adamovic in 1898 (Bur). **Bosnia:** southern, Trebevic, near Sarajevo, forest meadows, 1500–1600 m, Maly in 1903 (Bur). **Albania:** Maja Linerzit and Groppa Kostica, Baldacci 279 (K, Bur); montane forest near Diben, Dimonic in 1908 (UWH).

Relationship

Crepis viscidula shows considerable resemblance to *C. geracioides* in involucre, achenes, and pappus; and these 2 species are intermediate between *C. sibirica* and *C. lapsanoides* of sec. 3. The connection with *C. paludosa* is even closer on morphological grounds (cf. figs. 15, 16). But from their present distribution and that of secs. 3 and 5, it seems probable that *C. viscidula* and *C. geracioides* reached Europe from W. Asia by way of a southern route.

4. *Crepis paludosa* (L.) Moench

Meth. 535. 1794. (Figs. 16, 17.)

Perennial, 2.5–10 dm high, glabrous, except, usually, the inflorescence; rhizome short, stout, woody, vertical or oblique, densely fibrous; caudex leafy, bearing a stem of the season's growth and sometimes remnants of old stems; caudical leaves few, disappearing, 8–28 cm long, 3–5 cm wide, oblanceolate, acute, attenuate into a winged petiole, sinuate-dentate or denticulate, thin, dark green; lower cauline leaves similar or sessile; middle cauline leaves lanceolate to ovate, acute or acuminate, sessile, rounded-auriculate, amplexicaul; uppermost linear, bractlike; stem erect, often reddish near base, fistulose, sulcate, remotely leafy, branched above into a loose few-headed corymbiform cyme, branches pedunculate or 2–4-headed; peduncles 0.5–10 cm long, slender or rather stout, arcuate, glabrous or tomentulose or finely pubescent, subtending bracts often hairy; heads erect, medium, many-flowered; involucre cylindric, in largest heads 10–12 mm high, 4–6 mm wide, dark green, setulose, with long and short black or greenish hairs bearing brown glands, or rarely glabrous; outer bracts 10, unequal, longest about $\frac{1}{3}$ as long as inner ones, lanceolate, acuminate; inner bracts 16–20, in 2 equal or unequal ranks, lanceolate, sometimes strongly narrowed upward, acute, ciliate at the apex, glabrous within, with black dorsal median nerve becoming slightly carinate-indurate in fruit, never reflexed; receptacle naked; corolla 13–17 mm long; ligule 1.5–2 mm wide; teeth 0.3–0.7 mm long; corolla tube 3–4 mm long, glabrous or with a few very short papilliform trichomes; anther tube (3.5)4.25 \times 1 mm dis.; appendages 0.8 mm long, sagittate, acute; filaments long, unequal, longest filament attached at summit of corolla tube projecting beyond appendages 3 mm; style branches 1.75–2 mm long, 0.15 mm wide, acute, covered with dark green barbs except the plain, smooth, yellow stigmatic surface; achenes stramineous, 4.5–5.5 mm long, about 0.75 mm wide, columnar or slightly attenuate upward, \pm constricted below the pappus disk, strongly constricted near the pale oblique basal callus, 10-ribbed, ribs narrow, rounded, smooth; pappus pale yellowish, 6–7 mm long, 1-seriate, fine, rather brittle, scarcely exceeding the involucre. Flowering June–Sept.; flowers yellow, often described as pale yellow, but in fresh material collected in Yorkshire, England, the ligules were chrome-yellow, stamen tube yellow, with 5 purple ribs at maturity, style yellow, with dark green barbs. Chromosomes, $2n = 12$.

Hieracium paludosum L., Sp. Pl. 803. 1753.

H. paniculatum Gilib., Fl. Lithuan. 3: 236. 1781.

Aracium paludosum Monn., Ess. Hierac. 73. 1829.

Geracium paludosum Rehb., Fl. Excurs. 260. 1830–1832.

Soyeria paludosa Godr., Fl. Lorr. ed. 1, 72. 1843–1844.

Crepis caucasica C. A. Mey., Mem. Acad. Petersb. ser. vi, Sc. Nat. 7: 15. 1855.

C. glabra Boiss., Fl. Orient. 3: 843. 1875.

C. Ruprechtii Boiss., loc. cit.

C. rumicifolia Boiss., loc. cit.

Hieraciodes caucasicum O. Kuntze, Gen. 1: 345. 1891.

H. paludosum, *H. glabrum*, *H. Ruprechtii*, *H. rumicifolium* O. Kuntze, op. cit., 346. 1891.

Aracium attenuatum Opiz ex Domin, Preslia (Vest. Českoslov. Bot. Spol. Praha) 13–15: 251. 1935.

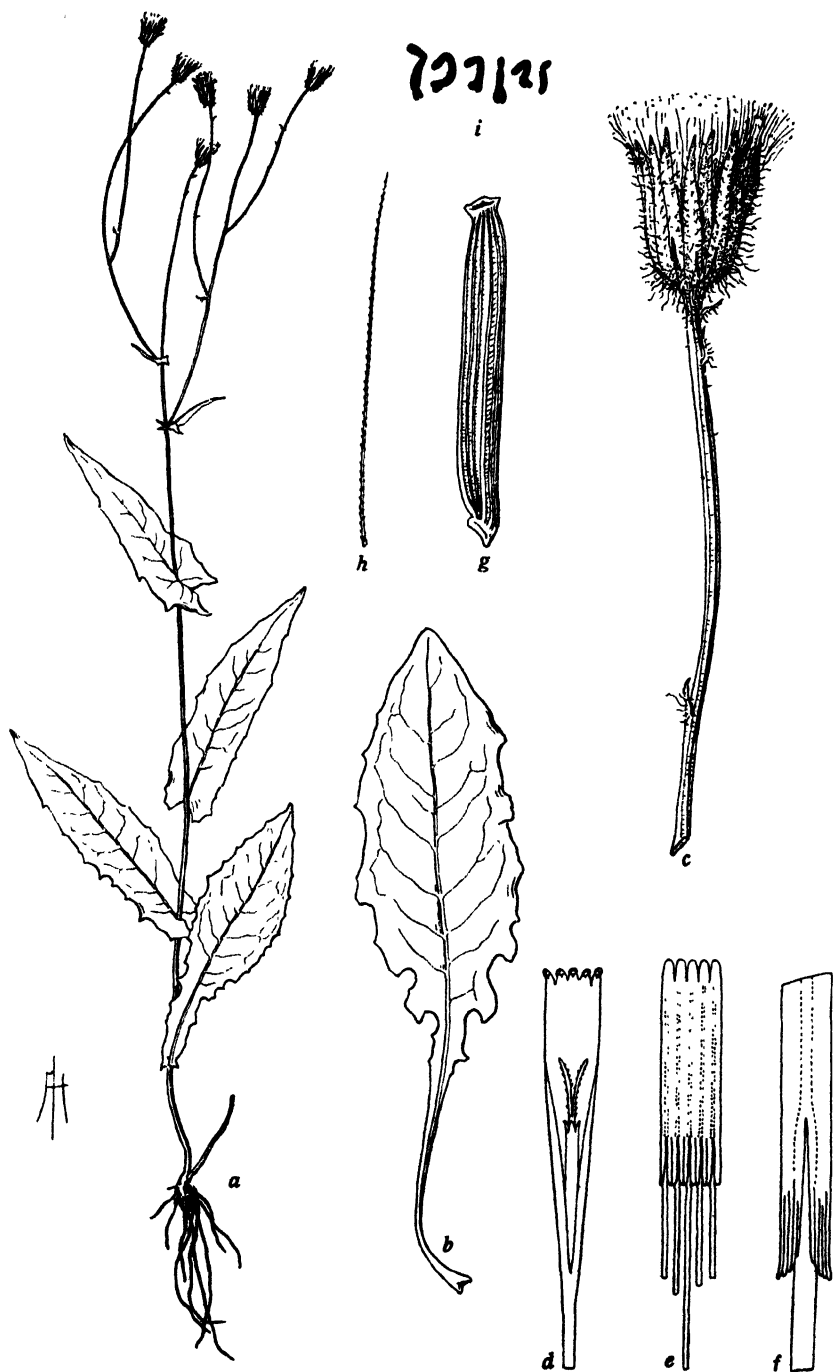


Fig. 16. *Crepis paludosa*, a–h, from Hjelt 399 (UC 250677); i, from hort. genet. Calif. 1825 (rhizomes received from Professor A. Thellung, Zurich): a, plant, $\times \frac{1}{4}$; b, basal leaf, $\times \frac{1}{2}$; c, head, $\times 2$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, h, achene and a pappus seta, $\times 8$; i, somatic chromosomes, $n = 6$, $\times 1250$.

A photograph of the type of Linnaeus (UC) shows young florets and no achenes. But this is a well-known and frequently illustrated species.

Most of Europe from the arctic regions southward into N. Spain and the Pyrenees, the mountains of central France, the Alps and N. Italy, the E. Balkan Pen., the Bulgarian Balkans and Rhodope Mts., the Carpathian Mts., the Caucasus and

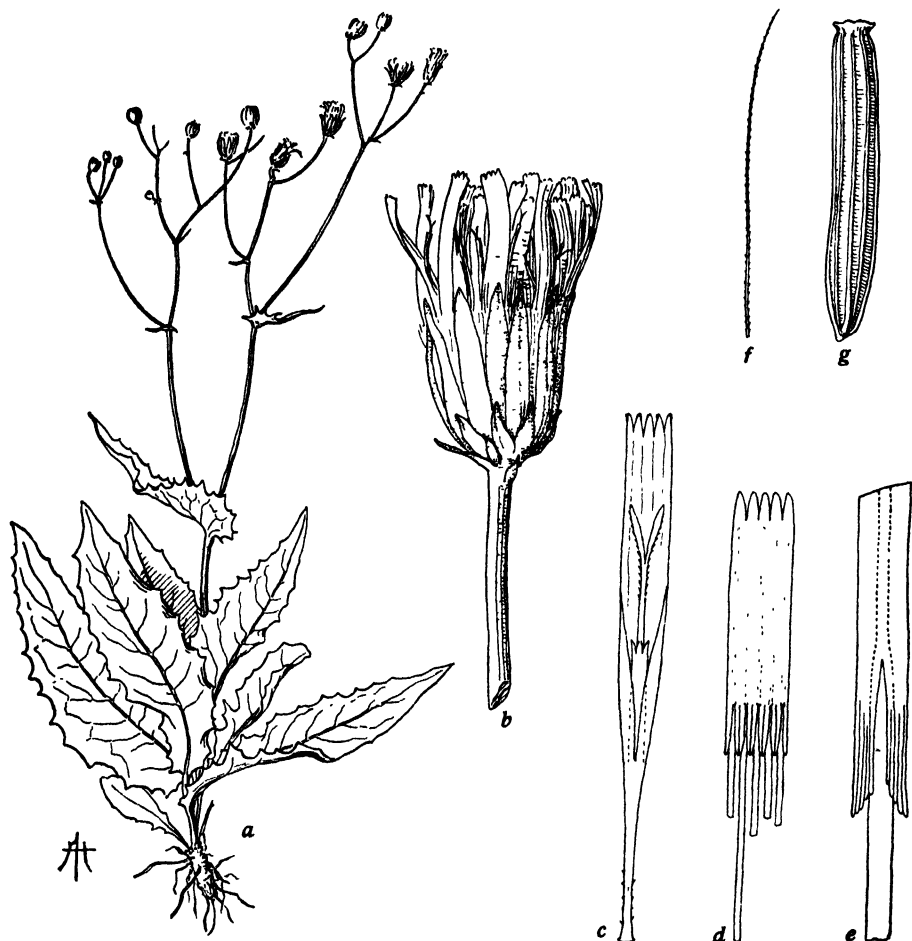


Fig. 17. *Crepis paludosa*, from type collection of *C. rumicifolia* Boiss. (Bo): *a*, plant, $\times \frac{1}{4}$; *b*, head, $\times 2$; *c*, floret lacking ovary, $\times 4$; *d*, anther tube, $\times 8$; *e*, detail of appendages, $\times 32$; *f*, *g*, achene and a pappus seta, $\times 8$.

Transcaucasia; W. Siberia. Usually found in moist places, in wet alpine meadows or bogs, near springs, streams, or lakes, often in forests; listed by Rübel (279) as a characteristic bog or swamp species, associated with *Juncus subnodulosus* and *Caltha palustris*. In the middle E. Swiss Alps, acc. to Braun-Blanquet and Rübel (1492), it occurs at elevations from 300 to 2150 m, but is most frequent in the subalpine zone. In S.W. Germany between Schwarzwald and Harz, acc. to Drude (141, 246), *C. paludosa* is very frequent on boggy places in all the higher mountains. The highest points in these mountains reach only 800 to 1100 m. Acc. to Pax (1: 109, 129; 2: 215), in the Carpathian Mts. this species is found in meadow bogs of lower hill lands and higher montane regions; and, in the Rodnaer Alps, above timber line on banks of brooks. It is found on both calcareous soils and soils

poor in lime. In Iceland this species is apparently autochthonous (cf. Gröntved, J., Reprint from "The Botany of Iceland" IV [1] : 371. 1942; Thorarinsson, S., *Geographiska Annaler* XIX [3/4] : 174. 1937).

Ireland: Wicklow, near Enniskerry, *Ball* (G). **Scotland:** Perthshire, Killicrankie Pass, *Lomaz* in 1887 (Minn). **England:** Yorkshire, Buttercambe, *Webster* in 1878 (UC). **Netherlands:** Burg Prov., Gulpen, *Tap* in 1907 (UC). **Belgium:** Limburg Prov., Geulle, *Tap* in 1919 (UC). **Germany:** Berlin, *Woller* in 1900 (UC, Minn). **Portugal** (?): "His. Lusit., Sierra del Chorro," *Durieu* 291 (DC). **Spain:** Soria-Logrona Prov., Sierra de Urbion, *Ceballos* in 1904 (UC); Pyrenees, Arran Valley, *Mouillefarine* in 1890 (US). **France:** Haute Garonne, Bagnères-de-Luchon, *Pellat* in 1899 (Grenoble); Puy de Dome, Mont Dore, *Pellat* in 1868 (Grenoble); Rhone, Vaugneray, *Saint-Lager* in 1877 (K); Vosges, Retourner Lake, *Raine* in 1905 (G). **Switzerland:** Fribourg, *Jaquel* in 1921 (DS); Engadine, St. Moritz, *Burnat* in 1873 (Bur); Central Alps, Davos, *Noack* in 1918 (G, Ms). **Austria:** Schwertberg, *Keck* (US, UC); Middle Styria, near Graz, *Heiderin* in 1907 (Bur); Upper Styria, Fraunalpe, near Murau, *Bajec* in 1900 (Minn). **Hungary:** Krassó-Szörény, baths of Hercules, *Thoisz* 3406 (G, Minn). **Czechoslovakia:** Louka slatina zópadně od Vroátka, *Celakovsky* in 1885 (PM); Brno, near Lisen, *Sua* 385 (US, UC). **Bulgaria:** near Sofia, Mt. Vitoscho, *Georgieff* 2907/I (UC); Rhodopes Mts., Mt. Pirin, "Kriva Bolta," *Stefanoff* in 1929 (UC). **Norway:** Flåstad, Lofoten, *Landmark* in 1899 (UC); Jederen, Haar, *Murbeck* in 1889 (Alger); Vestmarken, Sütre, *Luhr* in 1886 (Minn). **Sweden:** Angermanland, Solefteå, *Fries* in 1902 (US); Upsala dist., Björklänge, *Bågenholm* in 1904 (Minn). **Finland:** Ostrob, N. Kemi, Valmari, *Elmberg* in 1898 (US); Satakunta, Karkku, Järventaka, *Hjelt* in 1878 (UC). **Russia:** Lapland, Kola Pen., Ungin R., *Zinserling* 429 (Lenin); Olonetz Prov., Kiulmias R., *Iijin* in 1921 (Lenin); Smolensk Prov., Belsk Co., *Savicz* in 1926 (Lenin); Kostroma Prov., Buisk Co., *Kossinsky* 324 (Lenin); Novgorod Prov., Tichvinsk Co., *Kushnirenko* in 1924 (Lenin); Mohilew Prov., Mohilew, *Downar* in 1862 (Lenin); Iaroslav Prov., Roman Co., *Dmitriev* in 1900 (Lenin); Viatka Prov., Sarapul Co., *Alexandrov* 201 (Lenin); Perm Prov., Krassnonfimsk dist., *Korschinsky* in 1887 (Lenin); Ukraine, Chernigov Prov., near Klintsy, *Rogovitch* in 1854 (Lenin); Orenburg Prov., Troitzk Co., *Kysnetsov* 75 (Lenin). **Caucasus Reg.:** Caucasus Mts., near Kobi, C. A. Meyer in 1829-1830 (Lenin) m.v. 1; Lazistan, near Khabackar, 1900 m, *Balansa* 500b (Bo) m.v. 1; Caucasus, Mt. Utbiri, 2300 m, *Sommier et Levier* 830 (Fl) m.v. 1; Caucasus (central or eastern), Mt. Nakkerale of Tuschetia, 2200 m, *Ruprecht* (Bo) m.v. 2; Lazistan, above Khabackar, fir forest, *Balansa* 500, 500b (Bo, UCF) m.v. 4; Trebizond, Imbaschi, slope below Mt. Kisyl Ali Jaila, 1500-1600 m, *Handel-Mazzetti* 768 (UWG) m.v. 5.

Minor Variants of *Crepis paludosa*

In view of its wide distribution it is remarkable that *Crepis paludosa* is so stable. In a large series of specimens from various regions, of course some minor modifications appear. Also, forms like the following few, which are cited above, stand out rather strikingly: (1) Woller's Berlin plant (Minn), which grew on sandy clay soil and has unusually narrow, acuminate, upper cauline leaves and pale involucre hairs; (2) Georgieff's Bulgarian plant (UC) and Purpus' specimen (no. 115) from Smolensk, W. Russia (Lenin), both of which have perfectly glabrous involucres, corresponding in this respect to *C. paludosa* var. *glabrescens* Froel., in DC., Prod. 7: 170. But this and the other 3 varieties of Froelich which are listed by de Candolle are probably all insignificant variations.

In the Caucasus reg., however, several forms occur which are possibly of more significance. Four of these have been described as species. But because of their obviously close relationship to *C. paludosa*, sen. str., and the limited amount of material available, a very conservative treatment seems to be warranted. Accordingly, they are listed below as numbered variants, and a key is provided (p. 236).

1. (*C. caucasica* C. A. Mey., Mem. Acad. Petersb. ser. vi, Sc. Nat. 7: 15. 1855; *Hieraciodes caucasicum* O. Kuntze, Gen. 1: 345. 1891.) Plant 6-9 dm high, glabrous throughout; lower cauline leaves oblong, acute, upper ones lanceolate, acute or acuminate; stem few-branched near summit, few-headed; peduncles somewhat thickened near base of head; heads similar to typical forms except glabrous and perhaps a little larger; inner involucre bracts in 2 series, sometimes unequal; flowers, fruits, and pappus as in typical forms. C. A. Meyer in 1829-1830 (Lenin, photograph UC) near Kobi, Caucasus; *Balansa* 500b (Bo) near Khabackar, Lazistan; *Sommier et Levier* 830 (Fl) Mt. Utbiri, Caucasus.

2. (*C. glabra* Boiss., Fl. Orient. 3: 843. 1875; *Hieraciodes glabrum* O. Kuntze, Gen. 1: 346. 1891.) Plant 3–4 dm high, glabrous, except sometimes the involucre pubescent with long and short black gland hairs; lower cauline leaves oblong, acute, upper ones lanceolate, acute or acuminate; stem few-branched near summit, few-headed; peduncles somewhat thickened near base of head; heads similar to typical forms, except inner involucre bracts sometimes broader near tip; flowers, fruits, and pappus as in typical forms. *Ruprecht* (Bo, Ucf), Mt. Nakkerale, 2200 m, Tuschetia, central or E. Caucasus.

3. (*C. Ruprechtii* Boiss., Fl. Orient. 3: 843. 1875; *Hieraciodes Ruprechtii* O. Kuntze, Gen. 1: 346. 1891.) Plant (ex descr.) 3–4.5 dm high, \pm pubescent; lower cauline leaves larger than in m.v. 2, broadly ovate, obtuse, \pm setulose beneath; upper leaves equal to or shorter than peduncle, ovate-triangular; stem stiffly branched above, 2–3-headed, setose near base, setae flexuose, glandless; peduncles, at least lower ones, 10–13 cm long; heads larger than in m.v. 2; involucre greenish, inner bracts rather broad, obtuse, rather setose, outer bracts about $\frac{1}{2}$ as long as inner ones; achenes (immature) attenuate at summit; pappus sordid white. Specimen not seen, but it is stated by Boissier (sub *C. glabra*) that *C. glabra* forms a natural assemblage with *C. Ruprechtii*. Radde (370) reports *C. Ruprechtii* from Daghestan at 2000 m. The type, as cited by Boissier, was collected by Ruprecht in the forest-covered mountains of Antschabala, reg. of Tindal, 1800–2000 m, E. Caucasus.

4. (*C. rumicifolia* Boiss., Fl. Orient. 3: 843. 1875; *Hieraciodes rumicifolium* O. Kuntze, Gen. 1: 346. 1891.) Plant 4.5–7.5 dm high, glabrous throughout; basal leaves oblanceolate, acute, lyrate-pinnately divided, with very large terminal lobe and few lateral lobes, strongly attenuate into a narrowly winged petiole; cauline leaves mostly crowded near base, ovate, acute or acuminate, coarsely dentate, sessile, rounded-auriculate; stem branched from or above middle, branches long, strongly arcuate, few-headed; peduncles rather stout, somewhat thickened near head; heads somewhat larger than in most typical forms; inner involucre bracts in 2 notably unequal series; flowers, fruits, and pappus as in typical forms. (Fig. 17.) Radde (370) lists *C. rumicifolia* from Circassia at 2879 m. This district is in the W. Caucasus Mts., between the Black Sea and the Kuban R. *Balansa 500b* (Bo), forests of *Abies orientalis* above Khabackar, Lazistan (W. Caucasus reg., east of Pontus, near the Black Sea).

5. Resembles m.v. 2 in habit, only more extreme; plant about 4 dm high, glabrous throughout; lower leaves similar to m.v. 2, but more strongly congested at base of stem; all other cauline leaves reduced, lanceolate or linear; stem remotely branched from near middle, branches strict or fastigiate, 1–2-headed; peduncles rather stout, thickened near base of head; heads, fruits, and pappus similar to m.v. 2. It might at first appear that this and m.v. 2 represent an entity worthy of subspecific rank. But they come from widely separated regions and do not appear sufficiently distinct from typical forms of *C. paludosa* in their flowers and fruits. *Handel-Mazzetti 768* (UWG), montane depression, 1500–1600 m, north of Charshut R., between the villages Fol and Eseli, Imbaschi, slope below Mt. Kisyl Ali Jaila, Trebizond.

Key to the Caucasian Variants of *Crepis paludosa*

Stem branched near summit; middle and upper cauline leaves numerous, larger.

Lower cauline leaves oblong, acute; stem and leaves glabrous.

Plant taller (6–9 dm); involucre glabrous. 1. *caucasica*

Plant shorter (3–4 dm); involucre pubescent or glabrous 2. *glabra*

Lower cauline leaves ovate, obtuse; stem, leaves, and involucre \pm setulose; plant 3–4.5 dm 3. *Ruprechtii*

Stem branched near middle; middle and upper cauline leaves few or bractlike; lower cauline leaves ovate-acuminate or linear.

Basal leaves petiolate; branches and peduncles arcuate 4. *rumicifolia*

Basal leaves sessile; branches and peduncles strict or fastigiate 5. *m.v. 5*

Relationship

Crepis paludosa is a unique species. Its chromosomes are more like those of *C. viscidula* than those of any other 6-paired species; and in habit, leaves, and involucre it shows general resemblance to the species of sec. 1. But its achenes and pappus are more like those of *Hieracium*. The intermediate status of *C. paludosa* with reference to *Crepis* and *Hieracium* has long been recognized. The pappus is

typical of most species of *Hieracium*, whereas the fruits are really intermediate between *Hieracium* and *Crepis*, being more or less columnar, with a slight constriction at the summit. But the plant is *Crepis*-like and lacks the stellate pubescence and long shaggy hairs that are typical of *Hieracium*. Hence, on the basis of morphology, *C. paludosa* is predominantly *Crepis* but exhibits some characteristics of *Hieracium*.

In view of these facts, two general hypotheses concerning the origin of *C. paludosa* may be suggested: (1) the resemblance to *Hieracium* may be due simply to parallel evolution in the 2 genera, i.e., *C. paludosa* may have arisen from an ancestral stock which produced species of both *Crepis* and *Hieracium* through differentiation processes not involving interspecific hybridization, and (2) the resemblance to *Hieracium* may be the direct result of hybridization between a species of *Crepis* and one of *Hieracium* at a time when these species were still sufficiently close genetically to permit some degree of interfertility.

The first hypothesis may at first appear to be more plausible, but the second is worthy of consideration. If the *Crepis* parent had 6 pairs of chromosomes and the *Hieracium* parent 8 or 9 pairs, the only functional F_1 gametes would probably be those containing all or mostly all of either *Crepis* or *Hieracium* chromosomes. In *C. paludosa* the chromosomes are morphologically typical of 6-paired *Crepis* species, but there might have been an interchange of one segment between a *Crepis* and a *Hieracium* chromosome which provided *C. paludosa* with the genes conditioning its *Hieracium*-like achenes and pappus. Unfortunately, this species has proved to be very difficult to cultivate under artificial conditions. If some investigator could work with it under natural conditions, it might be possible to throw light on its evolutionary history through cytogenetic studies of artificial hybrids with closely related species and attempted crosses with certain species of *Hieracium*.

The assumption that the present distribution of *C. paludosa* had its beginning in a center of origin in N. Central Asia seems to favor a migrational history similar to that which has been proposed as the more probable one for *C. sibirica*. By penetration into N. Europe through the S. Ural reg. during the Miocene epoch, it could have spread clear across the continent and then moved southward during the gradual cooling of Pliocene and Pleistocene times to find refugial areas in central and S. Europe, including S. England and S.W. Norway, from which to establish its present wide distribution. During its wide-front advance southward it could have reached the Caucasian reg. where, during the Pleistocene uplift, conditions were favorable for the development of numerous distinct forms. This seems the more probable migrational history. It is also possible that, like its closest relative, *C. viscidula*, *C. paludosa* followed the Turano-Irano-Ponto-Balkan route, penetrating northward from Iran into the Caucasus reg. and spreading across S. Europe in preparation for its great trek northward in late Pleistocene and Recent times.

SECTION 2. SPATHOIDES

5. *Crepis kashmirica* Babc.

Univ. Calif. Publ. Bot. 14: 328. 1928. (Fig. 18.)

Perennial, about 3 dm high; rhizome woody, vertical and praemorse, or horizontal and somewhat elongated, with strong fleshy fibers; caudex slender, simple or divided, 1-2-stemmed, few-leaved; caudical and lower cauline leaves up to 12 cm long, 2.5 cm wide, oblanceolate, obtuse, irregularly denticulate, tapering into a winged petiole $\frac{1}{4}$ – $\frac{1}{2}$ as long as the blade with clasping base, gland-pubescent or tomentulose or glabrescent; upper cauline leaves lanceolate, acute, denticulate, sessile, subamplexicaul, shortly auriculate, \pm villous; stem rather robust, \pm curved, sulcate and glabrous or tomentulose below, striate and villous above, 3-4-branched near top, branches pedunculate; peduncles 1-4 cm long, thickened near base of head, and, like involucre, densely villous, with long glandless and short glandular hairs; heads erect, large, up to 50-flowered; involucre broadly campanulate, 10-15 mm long, 8-12 mm wide at middle, becoming indurate, otherwise little changed at maturity; outer involucre bracts 6-8, unequal, longest about $\frac{1}{3}$ as long as the inner, deltoid or lanceolate, acute; inner involucre bracts 14-20, in 2 or 3 ranks of equal length, lanceolate, acuminate, ciliate at apex, glabrous on inner face; receptacle areolate, areoles 0.5 mm wide, with a broad central stipe; corolla about 14 mm long; ligule 1.7 mm wide; teeth 0.5-1.5 mm long; corolla tube 3-4 mm long, glabrous; anther tube about 4.25×1.6 mm dis.; appendages 1 mm long, oblong, acute; filaments 1 mm longer; style branches 1.5 mm long, 0.1 mm wide, dark brown or black in sic.; achenes dark brown or black, pale yellow at the apex, 6-7 mm long, 1-1.5 mm wide at middle, fusiform, slightly attenuate to both ends, pappus disk 0.5 mm wide, 10-12-ribbed, ribs very prominent, rounded, smooth, base 0.4 mm wide, with prominent yellowish callus; pappus 7-8 mm long, of numerous dusky white bristles, 3-seriate, the setae very unequal in length and width, 20-60 μ wide at base, rather stiff, strongly persistent. Flowering July-Sept., flowers yellow. Chromosomes, $2n = 12$.

N. India, in the Kashmir, Hazara, and Lahul districts, in meadows, often near upper limit of birch forest, 3500-4300 m alt. Not common. A relic species (see fig. 12).

Monomorphic.

Himalaya (N.W.): Kashmir, Rajdianga, meadows at 3600 m, *Meebold 1059* (B) type; Kashmir, Sonamarg, 3500 m, *Clarke 30806* (K, Calcutta); Kashmir, above Gulmorg, 3600-3900 m, *Stewart 12717* (Mo); Kashmir, Tragbol Pass, 3600 m, *Stewart 4905* (UC); Kashmir, Sekiwas-Zaiwan, 3600 m, *Stewart 12387* (UC); Kashmir, Sonamarg, 3600 m, *Stewart 12382* (UC); Hazara, Kagan Valley, *Quayal 19751* (K); *ibid.*, *Duthie* (K, UC); Sar Saifar, Maluk Ka, 4360 m, *Kattha* in 1896 (DD); Lahul, Kukti Pass, alpine meadows, 3939 m, *Koelz 1180* (US).

Relationship

Crepis kashmirica is somewhat similar in habit to *C. blattarioides*, with which it was confused by Hooker (394); but it differs in nearly every detail, notably in the shorter strongly ribbed achenes, shorter florets, shorter anther tube, with longer acute appendages, the outer involucre bracts shorter, the receptacle not fimbriiferous, and the cauline leaves not auriculate. In leaves, involucres, and achenes it shows more resemblance to *C. sibirica* and *C. conyzaeifolia* than to *C. blattarioides*. It is very distinct from all other Himalayan species of *Crepis* at present known, and it has no very close relatives in the Old World. As in the other most primitive species of *Crepis*, the subcaudical part of the plant is a rhizome.

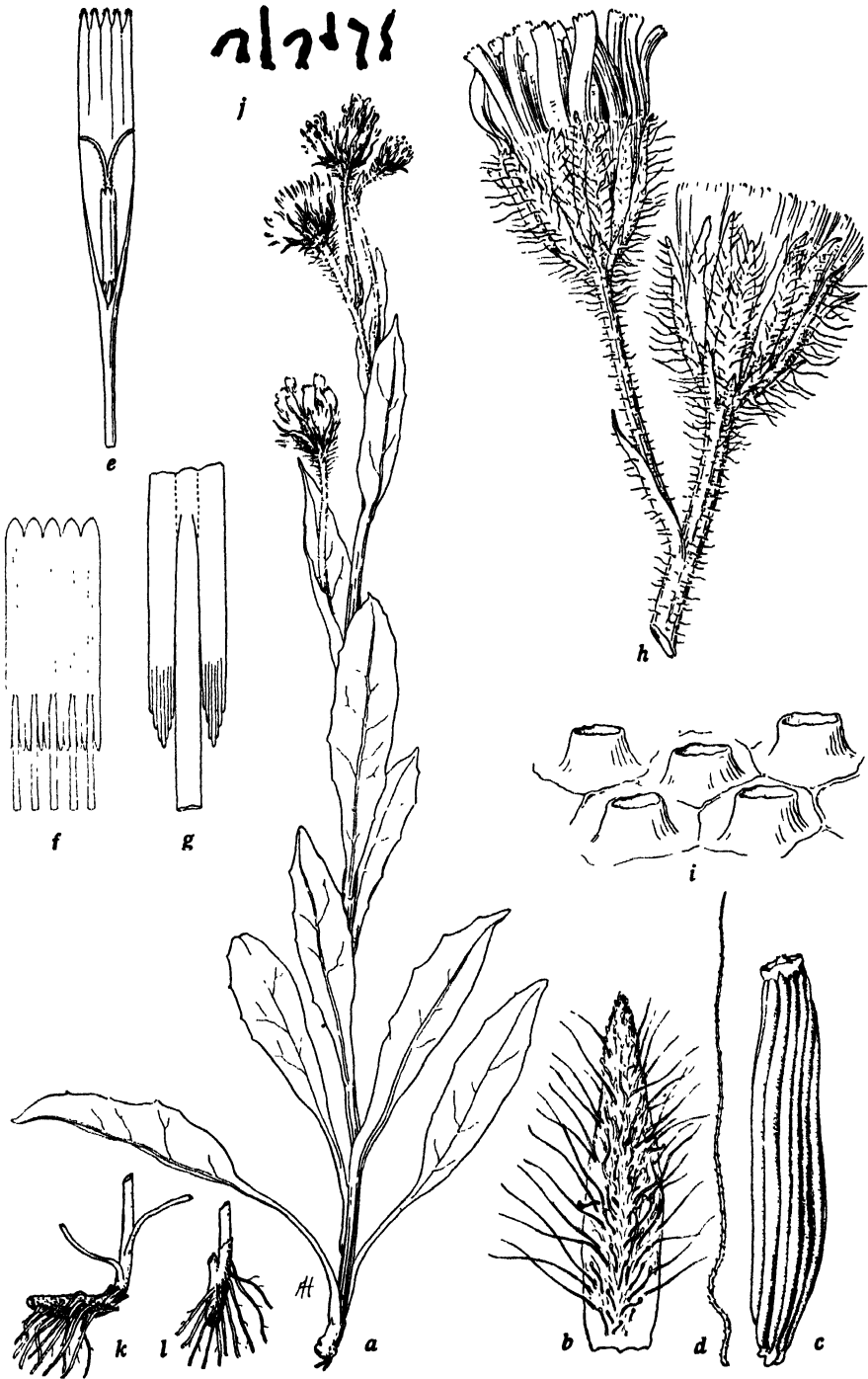


Fig. 18. *Crepis kashmirica*, a-d, from type (B); e-i, from Clarke 30806 (Calcutta); j-l, from Stewart 12382, 12387 (UC 476306, 476303): a, plant, $\times \frac{1}{2}$; b, inner involucre bract, outer face, $\times 4$; c, d, achene and a pappus seta, $\times 8$; e, floret lacking ovary, $\times 4$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, 2 heads, $\times 2$; i, detail of receptacle, $\times 25$; j, somatic chromosomes, $n = 6$, $\times 1250$; k, l, basal part of 2 plants, $\times \frac{1}{2}$.

This species nevertheless shows considerable resemblance to *C. monticola* of W. North America in shape of leaves and involueral bracts, in the hirsute peduncles and involucre, and in shape and ribbing of the achenes. It has been suggested (B. and S. 504: 30) that *C. kashmirica*, like *Dubyaea hispida* (Don) DC., may be closely related to one of the ancestors of *C. monticola*. This morphological evidence of a connection with a species which is certainly a relic and the origin of which can be referred to middle Tertiary times (*op. cit.*, p. 35) is an indication of the primitive nature of *C. kashmirica*. This species is somewhat more reduced than the 4-paired *C. blattarioides* in size of the outer involueral bracts and the florets; but it has the most prominently ribbed achenes of all the species in the genus, and strongly ribbed achenes are characteristic of other primitive *Crepis* species (cf. *C. sibirica*, *C. pontana*, *C. terglouensis*, *C. pygmaea*). It is also noteworthy that in *C. kashmirica* the marginal achenes are sometimes parthenocarpic and that these seedless fruits strongly resemble typical achenes of *Youngia* species in shape and ribbing. Normal marginal achenes of *C. kashmirica* retain this resemblance to some extent. Furthermore, the fact that the karyotype of this species is one of the two most primitive thus far known in *Crepis* (see Part I, pp. 11, 12, 65–66) is in good agreement with the conclusion that *C. kashmirica* is one of the most primitive species in the genus.

SECTION 3. OMALOCLINE

6. *Orepis pygmaea* L.

Sp. Pl. 2: 805. 1753. (Figs. 20, 21.)

Perennial, tufted, 0.4–2 dm high; rhizome branching, strongly fibrillate, terminated in a simple or divided caudex; leaves and stems grayish-green or \pm purple, canescent-tomentulose or densely tomentose, sometimes shortly and finely gland-pubescent; caudical leaves 3–11 cm long, 1–3 cm wide, lyrate-pinnately parted, with large elliptic rotund or ovate terminal segment and 2–4 small remote lateral segments, terminal lobe acute or obtuse, sinuately denticulate or nearly entire, cordate or rounded at base, lateral lobes lanceolate or triangular, acute, denticulate or entire, or these sometimes absent, making the leaves simple, spatulate, petiole 1–3 times longer than the terminal lobe, narrowly alate; cauline leaves numerous, similar, only slightly reduced; stem very short, or sometimes elongated, several times branched, the branches pedunculate or rarely 2-headed, erect or arcuate; peduncles erect or arcuate, striate, slightly enlarged, and usually densely tomentose near the head, 1–2-bracteate; heads erect, medium, 40–50-flowered; involucre campanulate, 10–19 mm long, 8–10 mm wide, canescent-tomentose or -tomentulose, often setulose with white or yellowish glandless setules; outer bracts linear, unequal, longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner; inner bracts lanceolate, membranous-margined, glabrous on inner face, becoming unchanged in color dorsally, but slightly swollen and, sometimes at least, definitely spongy-thickened at the very base when fully mature; receptacle areolate, very shortly white-ciliate; corolla, anther tube, and style branches yellow, the marginal florets often reddish-purple on outer face of ligule; achenes columnar to ellipsoidal as seen in widest plane, \pm attenuate upward, with slightly expanded pappus disk, thinly calloused at the small hollow base, 20–25-ribbed, ribs rounded, smooth; pappus whitish or tawny, 2–4-seriate, setae nearly equal in length and width, the coarsest about 80μ (8 cells) wide, rather soft but brittle at the base, persistent.

Mountains of Spain, France, Switzerland, N. and central Italy, and the Italian-Austrian Tirol (fig. 19). Acc. to Hegi (1146), *C. pygmaea* is a well-known colonizing pioneer on moist debris in the Alps of E. France and W. Switzerland. Like *C. terglouensis*, *C. rhaetica*, and *Leontodon montanus*, it contributes somewhat to the colonizing of recent deposits and moraines. However, it has been reported to me by M. Correvon of Genève (*in litt.*) to be very rare in the Alps; and this is confirmed by Melchior (Fedde Repert. Beih. 100: 173. 1938). But from the number of collections represented in Herb. Bar., it appears to be much more common in Spain, especially in the Pyrenees. This supports the contention of Melchior (*loc. cit.*) that *C. pygmaea* found its Pleistocene refugia in the western part of its present distributional area and has reached such eastern stations as the Brenta Alps (Trentino, N. Italy) by more recent migrations. Biologically, acc. to Hegi (*loc. cit.*), this plant is intermediate between the binding plants and the wanderers growing on debris. It usually occurs on calcareous formations and is found at altitudes from 1400 to 2800 m, under alpine or subalpine conditions, on exposed, sunny, well-drained soil. Braun-Blanquet and Rübel (1483) state that *C. pygmaea* is a basiphilous character species of the E. Rhaetic Alps (Swiss-Austrian frontier) occurring with *Thlaspeetum rotundifolium* in sliding calcareous gravel.

The type in Herb. Linné is illustrated in fig. 20, *a*. Because of its preference for loose, rocky, sometimes moving soil, the plant often grows up through the debris, lengthening the stem and sometimes the petioles and peduncles, thus making elon-

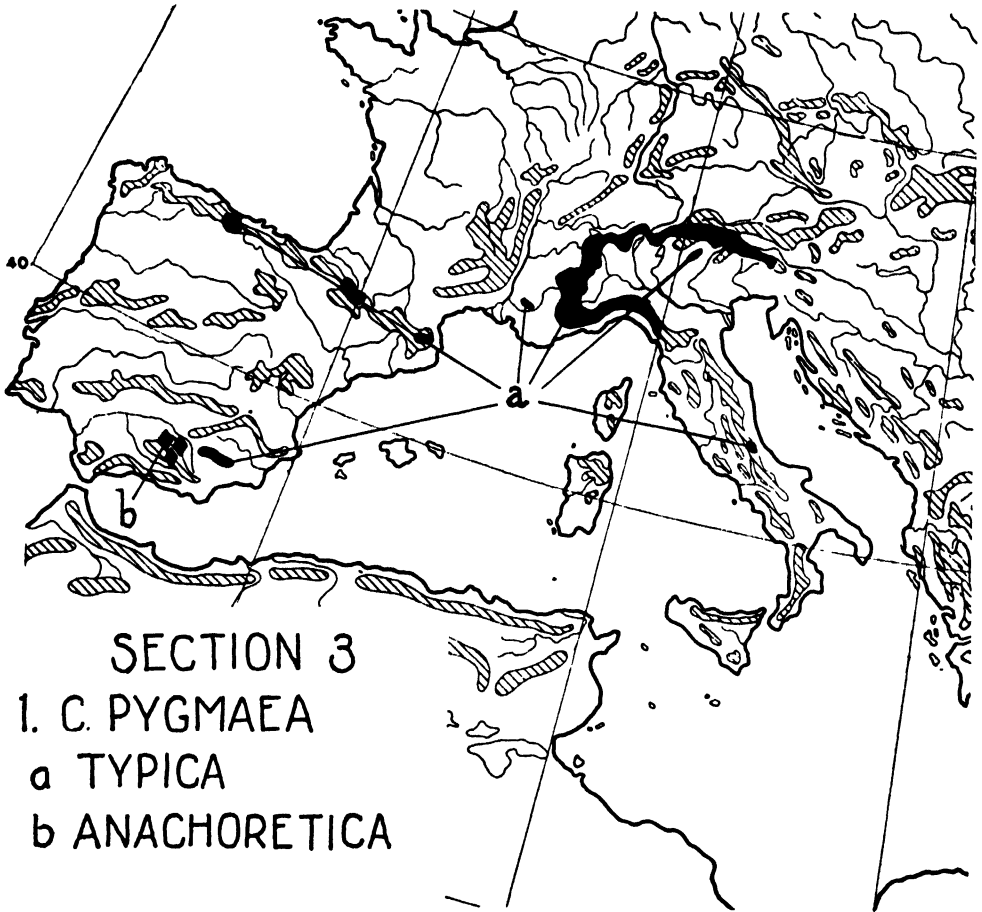


Fig. 19. Geographic distribution of *Crepis pygmaea*. The present disjunct distribution seems to indicate an older, more continuous range, although some of the stations may have been colonized comparatively recently. The 3 known stations for subsp. *anachoretica*, which is more primitive than subsp. *typica*, are shown by diamonds. Based on Goode Base Map No. 121. By permission of the University of Chicago Press.

gated tufts similar to those formed by *C. nana* under similar conditions. Some variability in leaf shape, amount of tomentum, and degree of glandulosity, as well as the amount of anthocyan pigment present, has been commonly observed. These minor variations have been used as the basis for a number of varieties by de Candolle (169), Fiori (437), and others. Much more important is the rather wide range in length of involucre, in size of florets and achenes, and in length of pappus. Although such variation is common throughout the range of the species, there has come to light in S. Spain an isolated entity in which the unusually large size of these parts is combined with a type of ribbing of the achenes which has not been observed in any other plants of this species. Such important differences call for the recognition of this entity as a subspecies.

Key to the Subspecies of Crepis pygmaea

- Involucres in fruiting heads 10–15 mm high; achenes 4–6.5 mm long, 20–25-ribbed, the ribs nearly equal; pappus 7–8 mm long 6, *a. typica*
 Involucres in fruiting heads, 16–19 mm high; achenes about 9 mm long, 20-ribbed, the ribs alternately wide and narrow; pappus 10 mm long 6, *b. anachoretica*

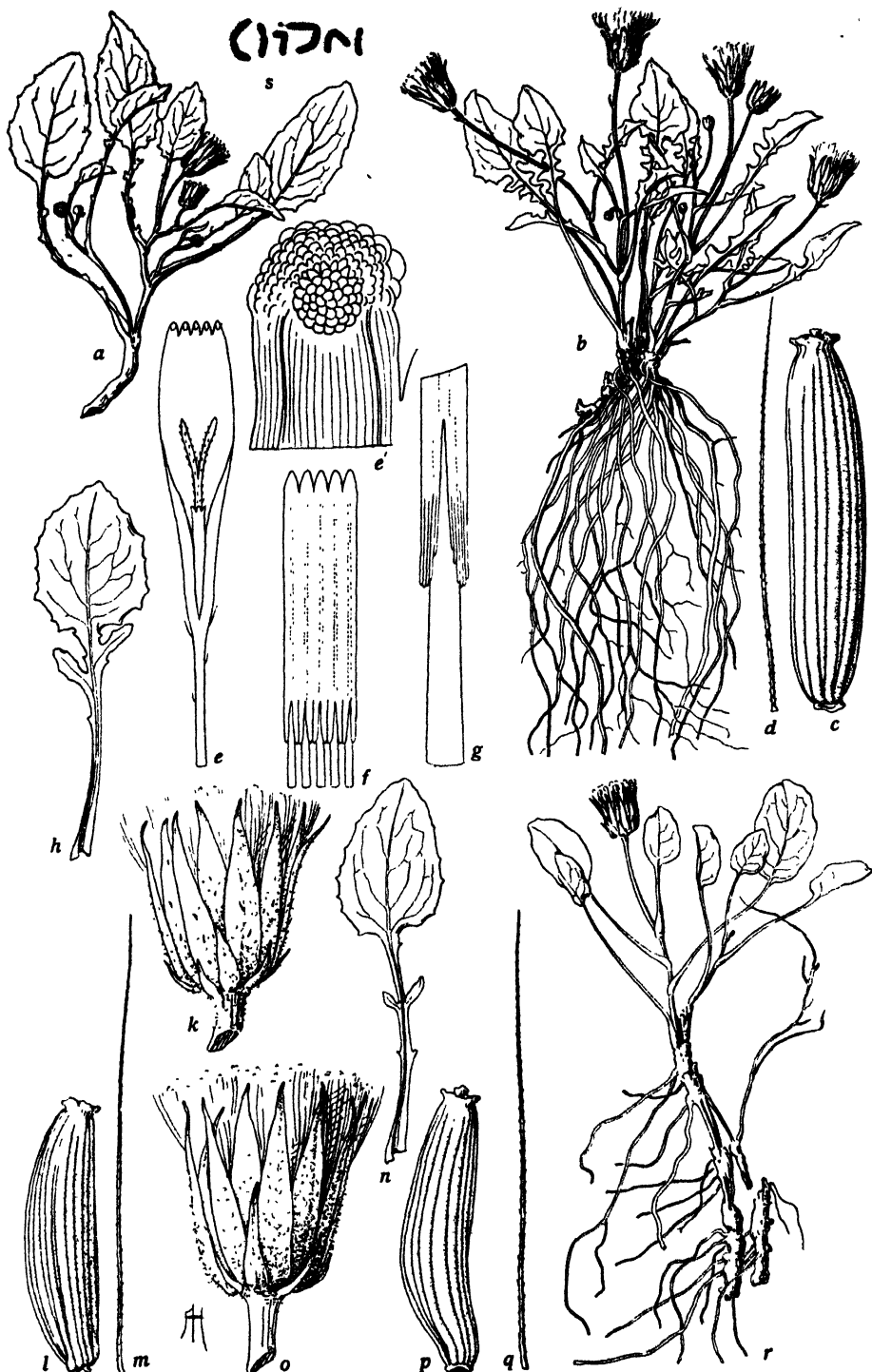


Fig. 20. *Crepis pygmaea typica*, a, from type (L); b-g, from Rigo in 1905 (UC 669414); h-m, from Faure in 1900 (UC 669415); n-r, from Scennen 1990 (UC 669417); s, from hort. genet. Calif. 3251 (roots received from Dr. G. Poirault, Director, Villa Thuret, Cap d'Antibes, France): a, upper part of plant, $\times \frac{1}{2}$; b, whole plant, $\times \frac{1}{2}$; c, d, achene and pappus seta, $\times 8$; e, floret lacking ovary, $\times 4$; e', detail of ligule tooth, $\times 50$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, leaf, $\times \frac{1}{2}$; k, head, $\times 2$; l, m, achene and pappus seta, $\times 8$; n, leaf, $\times \frac{1}{2}$; o, head, $\times 2$; p, q, achene and pappus seta, $\times 8$; r, plant, $\times \frac{1}{2}$; s, somatic chromosomes, $n = 6$, $\times 1250$.

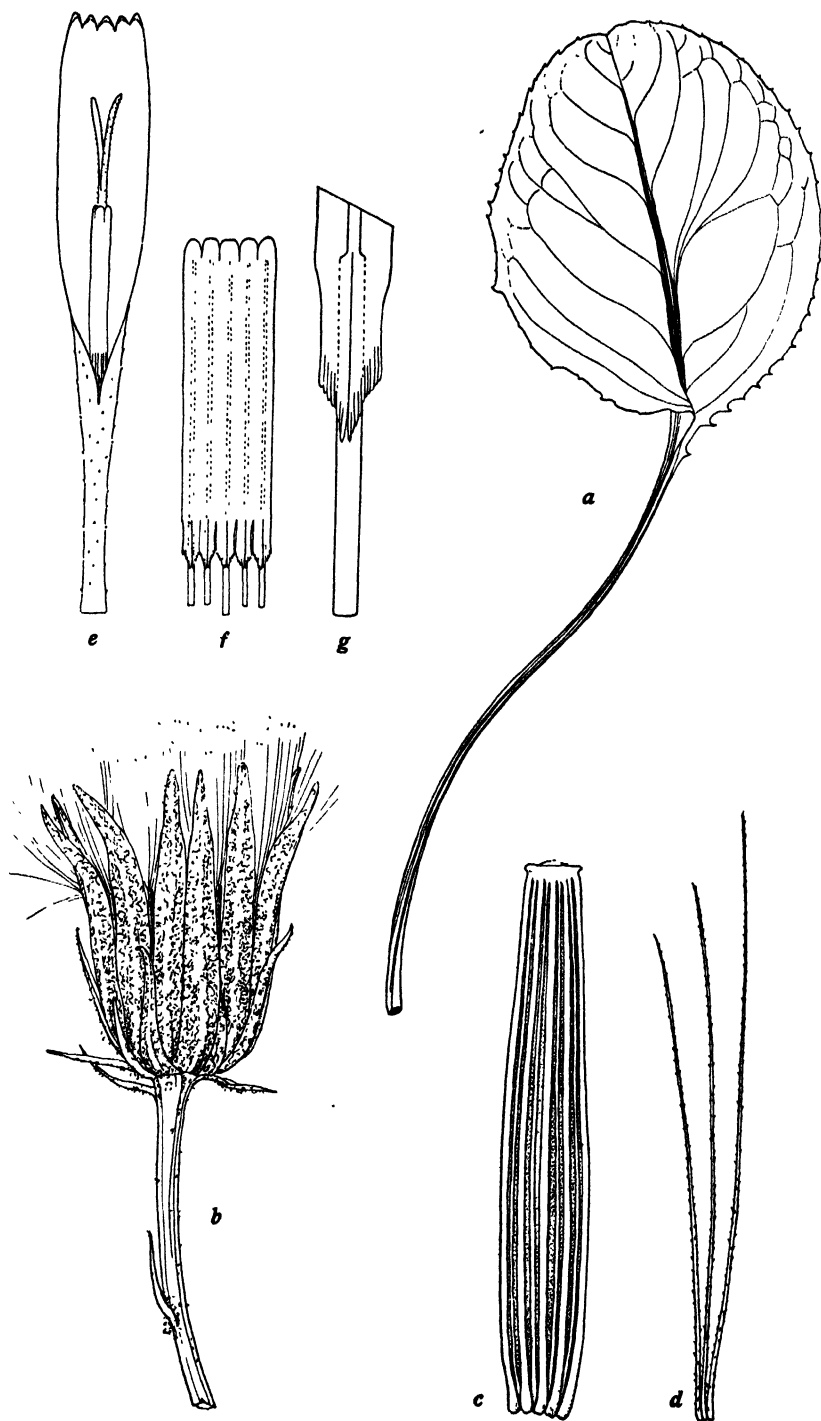


Fig. 21. *Crepis pygmaea anachoretica*, a-d, from type (UC 639611); e-g, from Cuatrecasas in 1926 (UC 639609): a, leaf, $\times 1$; b, fruiting head, $\times 2$; c, achene, $\times 8$; d, series of 3 pappus setae, $\times 8$; e, floret lacking ovary, $\times 4$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$.

6, *a. Crepis pygmaea typica* subsp. nov. Folia lyrato-pinnatifida interdum simplicia; pedunculi plerumque 3–8 cm longi; involucria 10–15 mm longa; corolla 15–16 mm longa; achaenia 4–6.5 mm longa, costatis aequalis; pappus 7–8 mm longus.

Leaves lyrate-pinnatifid or sometimes simple; peduncles 0.5–11 (mostly 3–8) cm long; involucries campanulate or cupuliform, 10–15 mm high, 7–10 mm wide at middle in fruit; outer bracts 7–12; inner bracts 12–16, acuminate or acute; corolla 15–16 mm long; ligule about 2.5 mm wide; teeth 0.3–0.5 mm long; corolla tube about 5 mm long, very sparsely pubescent, with coarse acicular hairs up to 0.5 mm long; anther tube about 5×1.5 mm dis.; appendages about 0.75 mm long, oblong, acute, or obtuse; filaments 0.75 mm longer; style branches 2–2.25 mm long, 0.2 mm wide, attenuate at tip, yellow; achenes light brown to dark reddish-brown, 4–6.5 mm long, 1–1.4 mm wide, somewhat obcompressed, slightly attenuate to both ends, or more definitely attenuate upward, the 20–25 ribs about equal, with occasionally a few weaker ones, not very prominent in fully mature fertile fruits; pappus 7–8 mm long, obscurely barbellulate. Flowering July–Sept. Chromosomes, $2n = 12$. See fig. 20.

Leontodon dentatus L., Mant. 1: 107. 1767.

Hieracium pumilum L., Mant. 2: 279. 1771.

H. prunellae-folium Gouan, Illustr. 57, t. 22, f. 3. 1773.

H. pygmaeum Lamk., Fl. Fr. 2: 100. 1778.

Lepicaune prunellae-folium Lapeyr., Abr. Pyr. 481. 1813.

Omalocline prunellae-folium Cass., Dict. 48: 431. 1827; Monn., Essai Hierac. 78. 1829.

Omalocline pygmaea Rehb. f., Ic. Fl. Germ. Helv. 19: t. 104, f. II. 1858–1859.

Hieraciodes pygmaeum O. Kuntze, Gen. 1: 346. 1891.

N. Spain in the Cordillera Cantabrica; S. Spain, Granada, in the Sierra Nevada; N.E. Spain and S.W. France in the Pyrenees; E. France in Hautes Savoie, Hautes Alpes, Basses Alpes, and Alpes Maritimes; Switzerland in Hautes Savoie, Vaud, Valais, Grisons, and the Berner, Rhaetic, and Engadin Alps; N. Italy in the mountains of Piedmont and Lombardy, and E. central Italy in the Majella Mts. In the Brenta Alps of Trentino, Lombardy, acc. to Melchior (Fedde Rep. Beih. 100: 174. 1938) this species occurs at about 2500 m alt., on loose calcareous debris with *Papaver pyrenaicum*, *Linaria alpina*, *Leontodon montanus*, etc. It is suggested that such alpine types moved up to their present levels from lower glacial refugia during the warm, dry postglacial period.

. The type, in the Linnaean Herbarium, London, is represented in Herb. UC by a photograph.

Spain: Cordillera Cantabrica, Leon, Mt. Espiguete, *Gandoger* in 1904 (Mo); Granada, Sagra Serra, in gravel, 2000–2400 m, *Porta et Rigo 571* (Bur); Catalonia, Pyrenees, Nuria, Noufons, schist, 2800 m, *Sennen 1990* (Bur, UC); *ibid.*, Serra del Cadi, 2200 m, *Font Quer* in 1926 (Bar, UC); E. Pyrenees, Nou Creus, 2800 m, *Cuatrecasas* in 1922 (Bar, UC); Nuria, Coma d'Eyne, 2700 m, *Cuatrecasas* in 1922 (Bar, UC). **France:** Basse Pyrenees, Eaux Bonnes, *J. Ball* (US); *ibid.*, Pic du Midi, *Bouget* (UC); Hautes Pyrenees, Cirque de Gavarnie, *Bodère* in 1868–1869 (Bur, US) and *Lomax* in 1888 (UC); Isère, La Salette, 1900 m, *Luny* in 1911 (UC); Drome, Mt. Ventoux, *Delacour* in 1876 (K) and *Pellat* in 1860 (Grenoble); Hautes Alpes, Lautaret, near La Grare, 1400 m, *Mathonet* in 1861 (Bur); *ibid.*, Mt. Durouze, 2200 m, *Faure* in 1900 (UC); Basses Alpes, Bougolières, *Proal 900* (Ms); Alpes de Provence, *Clarion* (DC) as *H. prunellae-folium*. **Switzerland:** Valais, Salanfe, col du Jorat, *Burnat et al.* in 1917 (Bur); Canton Wallis, Zaufleuron, 2350 m, *Fries* in 1909 (UC). **Italy:** Alpes Pedemont (PD) as *Berinea pygmaea* Tausch in herb.; Venezia, Friaul, Mt. Corno, *Martelli* (Po); Abruzzi, Canella Valley, 2000–2200 m, *Huet 375* (Bur); Abruzzi, Majella Mts., *Groves* in 1877 (K, UC); *ibid.*, 2000–2800 m, *Eigo* in 1905 (Po, UC).

6, *b. Crepis pygmaea anachoretica* subsp. nov. Folia simplices spathulata vel interdum lyrato-pinnatifida, segmentibus lateralibus 2–4 parvibus; pedunculi 4–20

cm longi; involucria in anthesi cupuliformia in fructu late cylindrico-campanulata et tum 16–19 mm longa ad medium circa 10 mm lata, squamis exterioribus 9–14, interioribus 12–14 acutis; corolla circa 20 mm longa, ligula 3–3.5 mm lata, tubo 6–7 mm longo minute pubescenti; antherae circa 5 mm longae flavae; rami styli 3 mm longi 0.2 mm lati flavi; achenia (non valde matura) straminea 9 mm longa 1.5 mm lata circa 20-costata, costis alternis latis et tenuis; pappus albus 10 mm longus dense barbellulatus persistens.

Leaves simple, spatulate, or sometimes lyrate-pinnatifid, with 2–4 small lateral lobes; peduncles 4–20 cm long; involucres cupuliform in anthesis, broadly cylindric-campanulate in fruit, and then 16–19 mm long, about 10 wide at middle; outer bracts 9–14; inner bracts 12–14, acute; corolla about 20 mm long; ligule 3–3.5 mm wide; teeth 0.3–1 mm long; corolla tube 6–7 mm long, beset with very short papilliform or acicular trichomes; anther tube 5.25×1.5 mm dis.; appendages 0.75 mm long, oblong, obliquely acute; filaments 0.5–0.75 mm longer; style branches 3 mm long, more than 0.2 mm wide, yellow; achenes (not fully mature) stramineous, 9 mm long, 1.5 mm wide, about 20-ribbed, *the ribs alternately wide and narrow*; pappus 10 mm long, densely barbellulate. Flowering July; flowers yellow, the marginal florets reddish-purple on outer face of ligule and suffused with red in sic. The name, *anachoretica*, connotes the primitive nature of this subspecies, as indicated by its habit, leaf shape, and involucres, and particularly by the alternately wide and narrow ribs on the achenes which resemble those of *Youngia depressa* as well as those of *C. sibirica*. See fig. 21.

Known only from the type region.

Spain: Jaen, Sierra Magina, El Almaden, 1800 m, *Cuatrecasas* in 1926 (UC 639611, Bar), type, isotype; Jaen, Magina, western part, 2050 m, *Cuatrecasas* in 1926 (Bar, UC); Sierra Magina, Carceles, 1900 m, *Cuatrecasas* in 1926 (UC, Bar).

Relationship

Crepis pygmaea is outstanding in its morphological resemblances to several species in other sections and even in different genera. In its low, tufted habit and spreading rhizomes it resembles *C. terglouensis*; its thick, prominently ribbed achenes are somewhat like those of the primitive species *C. kashmirica* and *C. terglouensis*; the resemblance of the ribbing of the achenes to that of *Y. depressa* and *C. sibirica* was noted above. A remarkable similarity has been noted also between the leaves, in all stages of ontogeny, of *C. pygmaea* and those of *Youngia depressa* (cf. B. and S., 484: 16, 35), which in turn shows relationship with the more primitive genera, *Dubyaea* and *Soroseris* (cf. Stebbins, 71–75). The low, tufted habit of *C. pygmaea* is also reminiscent of *Y. depressa* and the *Soroseris* species. This morphological evidence of a genetic connection between *C. pygmaea* and 3 other genera of S. Asia is very significant in connection with other evidence on origin and distribution of the genus derived from the study of chromosomes and geographic distribution.

SECTION 4. BRACHYPODES

Relationships of the Species

The species of this section are characterized by a short praemorse rhizome, low stature, pinnatifid or dentate leaves, scapiform stems, large or medium heads, villous or pubescent involucre, numerous florets, and beakless achenes. All 9 species are found in high montane locations, but they occur in widely separated regions. On the basis of morphological similarity the 9 species fall into 4 groups: (1) *C.*

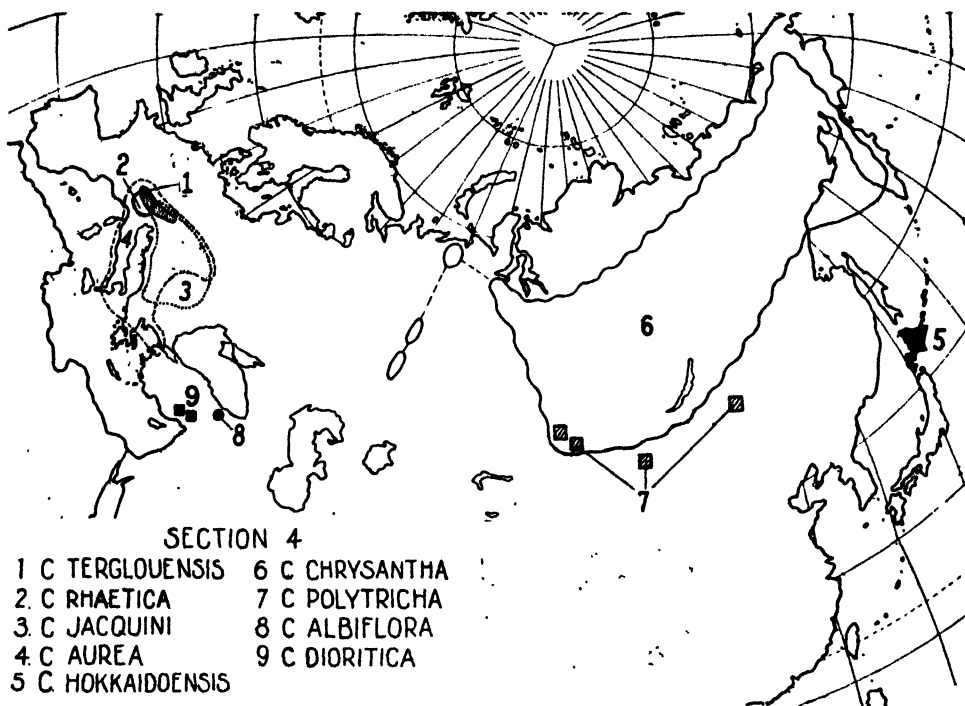


Fig. 22. Geographic distribution of the 9 species in sec. 4. *C. terglouensis* is restricted to the Swiss-Austrian Alps. *C. hokkaidoensis* is found only in N. Japan. One known station is shown by a solid circle; 2 known stations, by solid squares; 4 stations, by shaded squares. Based on Goode Base Map No. 201 PC. By permission of the University of Chicago Press.

terglouensis, *C. rhaetica*; (2) *C. Jacquini*, *C. aurea*, *C. chrysantha*, *C. polytricha*; (3) *C. hokkaidoensis*; (4) *C. albiflora*, *C. dioritica*.

1. *C. terglouensis* and *C. rhaetica* are certainly the most primitive species in the section and are among the most primitive in the genus. The karyotype of the former (see fig. 23) is more primitive, at least on the basis of chromosome size, than that of *C. pygmaea*, but the plant does not exhibit as many resemblances to primitive species of other genera as does *C. rhaetica*. The primitive nature and restricted distribution of these 2 species (central European Alps) mark them as relics.

2. The 4 species in the second group show sufficient resemblance, notably in their leaves and fruits, to indicate fairly close relationship. This is especially interesting because each species has a different chromosome number. On the well-established basis of karyotype evolution in this genus (see Part I, p. 11), *C. Jacquini*, with $n = 6$, has a primitive karyotype resembling that of *C. terglouensis*. *C. aurea*, with a haploid number of 5 and more asymmetrical chromosomes, represents an intermediate phylogenetic stage between *C. Jacquini* and *C. chrysantha*. *C. chrysantha*, with

$n = 4$, represents a later stage than *C. aurea*, but a stage antecedent to that of *C. polytricha*, which is a tetraploid with $x = 4$. The distribution of *C. Jacquini* and *C. aurea* in central and E. Europe and of *C. chrysantha* and *C. polytricha* in Central and N. E. Asia (see fig. 22) is not inconsistent with the hypothesis that Central Asia was the region of origin of the genus. Considerable morphological resemblance exists between this group and the more advanced species of sec. 14.

3. *C. hokkaidoensis* seems to have had a similar distributional history to that of *C. chrysantha* and *C. polytricha*. Like them, it differs from the other species in the section in having the inner involucreal bracts pubescent on the inner face. But its long-necked, weakly ribbed fruits are unique in this section; and this feature, together with its leaf shape and hairiness, suggests a relationship with the American species, *C. modocensis*. In this connection, its present distribution in N. Japan is of special significance.

4. *C. albiflora* and *C. dioritica* are the most reduced species in the section; this is shown by their bipinnate leaves, more slender stems and smaller heads, florets, and achenes. Their close connection with any other species is not evident. *C. albiflora* has 4 pairs of chromosomes. The fact that the distribution of these species is in Asia Minor, whereas the more primitive species in the section are distributed peripherally with reference to Central Asia, is a situation in agreement with Matthew's principle (see Part I, p. 75).

Key to the Species of Section 4

- Plants 0.2–0.9 dm high; cauline leaves closely spaced, approaching the caudical leaves in size.
- Leaves pinnatifid; florets about 19 mm long; achenes oblong or cuneiform, yellow, finely speckled with purple or black. 7. *C. terglouensis*, p. 249
 - Leaves entire; florets about 13 mm long; achenes gradually attenuate to the apex, reddish-brown 8. *C. rhaetica*, p. 251
- Plants mostly 1–2 (rarely 0.2–3) dm high; cauline leaves 0–2 or, if several (*C. Jacquini*), mostly remote and reduced.
- Stems leafless, 1–2-bracteate; outer involucreal bracts $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner, or if $\frac{2}{3}$ as long (*C. albiflora*), then the flowers white.
 - Flowers deep yellow, orange, or red; leaves dentate to pinnatifid, the lobes not dentate, glabrous 11. *C. aurea*, p. 260
 - Flowers white or pale yellow; leaves pinnately parted, the lobes dentate, pubescent.
 - Flowers white; heads many-flowered; style branches 2.5 mm long; achenes tawny 14. *C. albiflora*, p. 267
 - Flowers pale yellow; heads 15–20-flowered; style branches 1–1.5 mm long; achenes dark brown 15. *C. dioritica*, p. 269
 - Stems bearing 1 or more leaves; outer involucreal bracts $\frac{1}{2}$ – $\frac{2}{3}$ as long as the inner; flowers yellow.
 - Cauline leaves several, remotely pinnately parted with narrow segments; inner involucreal bracts glabrous on inner face; corolla tube glabrous. 9. *C. Jacquini*, p. 255
 - Cauline leaves 1–2, entire or dentate; inner involucreal bracts pubescent or strigulose on inner face; corolla tube pubescent (or rarely glabrous in *C. polytricha*).
 - Inner involucreal bracts densely strigulose on inner face, with white, shining trichomes; achenes 7.5–10 mm long, gradually attenuate upward into a neck, dark brown, the neck paler. 10. *C. hokkaidoensis*, p. 257
 - Inner involucreal bracts silky-pubescent on inner face; achenes 5–9.5 mm long, reddish-brown or purplish.
 - Involucreal hairs mostly straight, dark or pale green, glandless; corolla 13–19 mm long; achenes reddish-brown or dark purple, 5–9.5 mm long, 15-ribbed; pappus 5–8 mm long, rather fine. 12. *C. chrysantha*, p. 263
 - Involucreal hairs crinkled, greenish-yellow, glandless, together with shorter, green, glandular ones; corolla 18–25 mm long; achenes dark purplish, 7 mm long, 20-ribbed; pappus 8 mm long, rather coarse 13. *C. polytricha*, p. 265

7. *Crepis terglouensis* (Hacq.) A. Kern.

Sched. Fl. Exsicc. 61. 1863–1869. (Fig. 23.)

Perennial, 0.2–0.6 dm high; rhizome vertical or oblique, praemorse, brown-sealy, fibrillate; caudex narrow, short, leafy, 1-stemmed; caudical leaves 2–7 cm long, 0.6–1.5 cm wide, oblanceolate, obtuse, sometimes mucronate, runcinately dentate to pinnatifid, with triangular or roundish lobes and curved sinuses, the lobes often somewhat retrorse, petiole very short or equal to the blade, narrowly winged, broader at base, bright green, thickish, glabrous or pubescent beneath; cauline leaves several, closely spaced, similar to the caudical or slightly broader, acute or acuminate, uppermost linear, entire, densely hairy with yellow or greenish glandless hairs; stem erect, 1-headed, terete, thickened, and villous near head; head often surrounded by upper cauline leaves, erect, large, about 60-flowered; involucre nearly half-globose, 7–14 (20) mm high, 7–12 (18) mm wide at middle in anthesis, little changed in fruit, blackish-green, densely villous with dark green glandless hairs; outer bracts 9–12, unequal, from $\frac{1}{2}$ – $\frac{3}{4}$ as long as the inner, linear to lanceolate, acute or obtuse; inner bracts 12–20, lanceolate, acute, or acuminate, densely white-ciliate at apex, glabrous on inner face, becoming somewhat thickened and (?) indurate at full maturity; receptacle convex, areolate, glabrous; corolla about 19 mm long; ligule 3 mm wide; teeth about 1 mm long; corolla tube about 5 mm long, sparsely beset with very short stout 2–4-celled trichomes; anther tube 6×1.3 mm dis.; appendages 1 mm long, oblong, obtuse; style branches 2.5–3 mm long, 0.2 mm wide, gradually attenuate, yellow; achenes yellow, finely speckled with purple or black, 3.5–5 mm long, 1–1.25 mm wide, oblong or cuneiform, truncate at both ends, abruptly constricted at summit, the unexpanded pappus disk broad and white, more gradually narrowed to the thinly calloused hollow base, subterete or somewhat compressed or obcompressed, 10–13-ribbed, ribs nearly equal, very prominent, rounded, smooth; pappus white, 8 mm long, 2-seriate, setae in outer series very coarse, up to 130μ (8 cells) wide, rather stiff and brittle, persistent. Flowering Aug.; flowers golden yellow. Chromosomes $2n = 12$.

Leontodon terglouensis Hacq., Pl. Carn. 11, t. 2, f. 5. 1782.

Hieracium hyoseridifolium Vill., ex Pers., Syn. 2: 370. 1807.

Crepis hyoseridifolia Rchb., ex Moessl., Handb. ed. 2, 2: 1403. 1827–1829; Tausch, Flora 11 (1 Erg.): 79. 1828.

Apargia hyoseridifolia Less., Syn. Comp. 132. 1832, *ide* DC., Prod. 7: 171. 1838.

Soyeria hyoseridifolia Koch, Syn. Fl. Germ. ed. 1, 442. 1837.

Hieraciodes terglouense O. Kuntze, Gen. 1: 345. 1891.

Named (acc. to Hegi, 1143) after the Triglav in Krain, the highest peak of the Julian Alps, which has been known as Terglou since Napoleon's time.

The type has not been seen by me, but authentic specimens of Kerner are cited below.

Alps of Upper Austria and central Tirol and westward through the Swiss Alps to Valais and Freiberg. Acc. to Hegi (*loc. cit.*), this species always occurs on calcareous formations in alpine situations (1800–2800 m) up to the snow line; and it is gregarious in resting debris and fine-grained debris of slopes; seldom in moving gravel. It is a very distinctive monomorphic species of the E. "Kalkalpen," occurring in Switzerland only on high crags. Canton Freiberg is the western limit of distribution. Hegi (*loc. cit.*) states that the plant is similar in general appearance to *Leontodon montanus*, with which it occurs; and apparently the latter species was mistakenly illustrated as *C. terglouensis* by Hegi (*op. cit.*, 1143 f. 820, 1144 f. 821, wherein are shown the narrow involucre and the leaf shape of the plants).

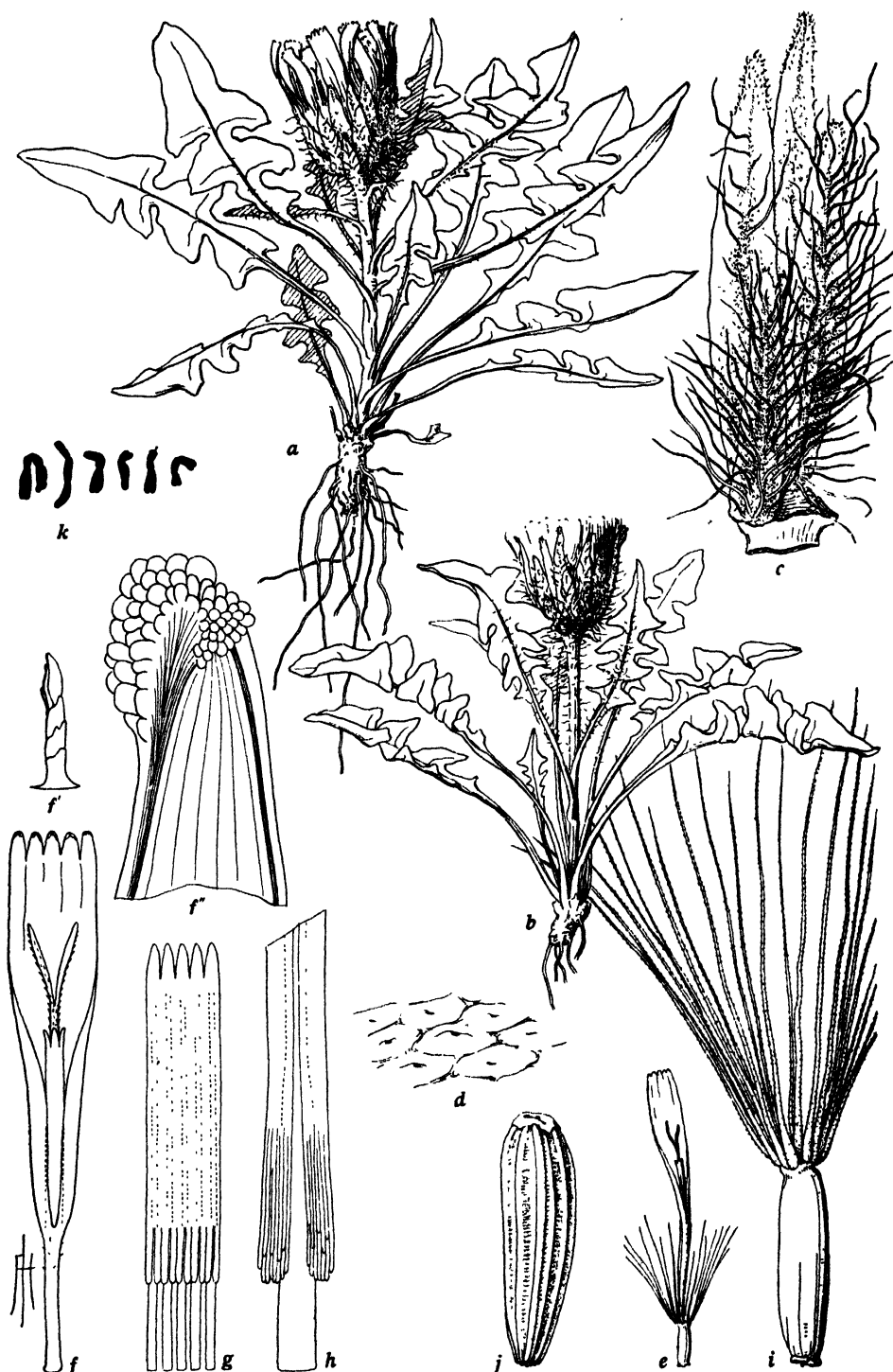


Fig. 23. *Crepis terglouensis*, a, from Woynar in 1887 (Minn 217816); b-i, from Cohrs in 1930 (UC 463914); j, from Bot. Gard. Univ. Innsbruck (UC 322840); k, from hort. genet. Calif. 3414 (seeds received from University of Innsbruck): a, b, plants, $\times 1$; c, 4 involucre bracts united at base, outer face, $\times 4$; d, detail of receptacle, $\times 25$; e, floret, dry, $\times 2$; f, floret lacking ovary, $\times 4$; f', trichome from corolla tube, $\times 50$; f'', detail of ligule tooth, $\times 50$; g, anther tube, $\times 8$; h, detail of appendages, $\times 32$; i, immature achene, $\times 8$; j, mature achene, $\times 8$; k, somatic chromosomes, $n = 6$, $\times 1250$.

Austria: Upper Austria, near Windischgarsten, *Oberleitner* in 1863 (DS, UC); Belkengrab, Rhaetikon, *Horck* in 1902 (Bur); Carinthia, Speckweise, and Warscheneck, near Windischgarsten, *Oberleitner* in 1863 (Bur); Almajurjoch, near Arlberg, *Colers* in 1930 (UC); N. Tirol, Markspitze am Sonnenwenjoch, *Wojnar* in 1887 (Minn); Mt. Blaser, near Matrei, *Obriest* 197 (Bur); *ibid.*, *Kerner* in 1869 (UWK, US) authentic specimens; Vorarlberg, *Horck* (Po); Lower Austria, *Beck* in 1887 (Ms); central Tirol, Gschnitzthal, Trins, highest part of Sadailalen, *Churchill* in 1873 (K), with *C. Jacquini* and *C. hybrida*; Gschnitzthal, Magdalenenthal, southwest corner of summit of Muttenjoch, *Churchill* in 1873 (K). **Italy:** central Tirol, Platzerberg, above Gossensass, *Huter* in 1889 (Bur); Mt. Riedberg, near Sterzing, *Huter* in 1887 (Bur, Grenoble); Mt. Hühnerspiele, near Gossensass, *Kerner* in 1868 (UWK). **Switzerland:** Rawyl, toward Bernois, *Castella* in 1905 (US); Grisons, Churer Fochs (Bur); Säntis, Appenzell, *Muret* in 1842 (Bur); Vanil, Gruyère (Bur); Freiberg, Algan, *Christen* (Bur); Freiberg, Moléson, *Sandoz* in 1861 (Bur).

Relationship

Crepis terglouensis, on the basis of size of heads, florets, achenes, and the outer involucre bracts, is the most primitive species of this section. Although the achenes of *C. Jacquini* sometimes have more numerous and unequal ribs, yet the achenes of *C. terglouensis* have unusually strong ribs and the pappus is much coarser. In spite of their many differences the 2 plants are obviously related and their chromosomes are in general very closely similar in size and shape.

Natural hybrids occur between *C. terglouensis* and *C. Jacquini* apparently wherever the 2 species meet (cf. $\times C. hybrida$ A. Kern.), but it is unlikely that these hybrids have more than a very low degree of fertility. It is known that a natural hybrid between *C. blattarioides* and *C. alpestris* was completely sterile under favorable garden conditions. Although *C. terglouensis* and *C. Jacquini* are not quite so unlike as the other 2 species just mentioned, yet they differ strikingly in nearly every part of the plant. It may be noted that *Huter* (Oesterr. Bot. Zeitschr. 57: 113, 1907) states that *C. hybrida* is polymorphic, being sometimes exactly intermediate and sometimes more like one or the other parent. This can be explained as due either to heterozygosity of the parents or the occasional production of viable seeds by F_1 hybrids. A number of herbarium specimens which I have seen in various herbaria agreed very well with the intermediate nature of *C. hybrida* as described by *Kerner*. After all, the 2 species actually come into contact in relatively few places, and there is nothing to indicate that even in those places the natural hybrids are tending to swamp out either species.

C. terglouensis, like *C. pygmaea*, is undoubtedly a primitive species. Although it does not exhibit as many definite similarities to primitive species of other genera as does *C. pygmaea*, yet the tufted habit is reminiscent of *Youngia* and *Soroscris*, and, although very different in shape, the peculiarly mottled achenes resemble those of *Y. depressa* in color. Furthermore, the large flower head, the villous involucre with long outer bracts, the large florets, strongly ribbed achenes, and very coarse pappus setae are certainly indicative of primitiveness.

8. *Crepis rhaetica* Hegetschw.

Fl. Schweiz, 769, 1840, non Nyman, Consp. 456, 1879. (Fig. 24.)

Perennial, 0.2–0.9 dm high; rhizome variable in length; in old, well-developed plants it may be more than 9 cm long, oblique, with fleshy fibers and furcate near the summit; in young plants it is short and praemorse, with a single caudex; caudex bearing 1 stem, brown-scaly, leafy at crown; caudical leaves few, congested, 2–5 cm long, 0.5–1 cm wide, oblanceolate, obtuse, sometimes apiculate, entire, or weakly denticulate, attenuate into a short winged petiole, glabrous or puberulent; cauline leaves 1–2, small, lance-linear, acute, sessile, like stem \pm hairy; stem erect, scapiform, gradually thickened toward the head, densely pubescent, with yellow or

greenish glandless hairs which become longer near the head; heads erect, medium, 35–40-flowered; involucre campanulate, 11–13 mm high, about 10 mm wide at middle in fruit, dark green, very densely hirsute, with fine long green glandless hairs; outer bracts about 6–9, unequal, longest $\frac{1}{2}$ – $\frac{2}{3}$ as long as inner bracts, lanceolate, acute, or acuminate; inner bracts 12–16, lanceolate acute, sparsely strigulose on inner face, with short shining trichomes, not at all thickened at early maturity; receptacle areolate, shortly white-ciliate; corolla about 13 mm long; ligule 2 mm wide; teeth 0.2–0.4 mm long; corolla tube about 5 mm long, pubescent, with coarse acicular hairs 0.05–0.8 mm long; anther tube about 3.5×1 mm dis.; appendages 0.7 mm long, oblong, acute; filaments 1–1.5 mm longer; style branches 1.5 mm long, 0.15 mm wide, attenuate, yellow; achenes brown, 6 mm long, about 0.7 mm wide, columnar, gradually attenuate upward, with expanded pappus disk, constricted near the lightly calloused, hollow base, 18–20-ribbed, ribs in mature fruits alternately wider and narrower, rounded, smooth, or muriculate under lens; pappus dusky or yellowish-white, 6–7 mm long, 2-seriate, setae about equally fine, 30–45 μ wide at base, rather firm but pliable, persistent. Flowering July–Aug.; flowers yellow.

Crepis Heerii Moritz, Pfl. Graub. 87. 1839, nom. nud.

C. jubata Koch, Taschenb. 321. 1844.

C. chrysantha Koch, Synopsis ed. 2, 2: 503. 1844, non (Ledeb.) Froel., ex DC., Prod. 7: 165. 1838.

Soyeria rhaetica Ducommun, Taschenb. Schweiz Bot. 455. 1869.

S. jubata Rouy, Fl. Fr. 9: 232. 1905.

Central European Alps; mostly in Italian Tirol and Switzerland; also reported from Austrian Tirol and from Mt. Iseran in Savoie; alpine and subalpine.

This species, acc. to Braun-Blanquet and Rübel (1485), is very rare and scattered in the upper alpine zone from 2500–2900 m in the middle E. Swiss Alps; and it grows on exposed, resting detritus of calcareous formation. Acc. to Hegi (1147), this plant occurs singly or in mats, on ridges in rock debris, in loose "pioneer turfs," and between slabs of rock. In Tirol it occurs from above snow line to more than 3000 m, in Valais to 2800 m; only exceptionally is it abundant at subalpine elevations, as in Tirol at Fimberjoch at 1950 m. It is found on calcareous rock, on "Grisons schist," and on Verrucano (a peculiar conglomerate found in the Alps, which, although associated with carboniferous deposits, is a local phase of deposition persisting through more than one period). Hegi states (*loc. cit.*) that the sporadic and restricted distribution of this species characterizes it as a relic of the central Alps, like *Carex alpina*, *Juncus artica*, *Ranunculus pygmaea*, *Viola Cenisia*, etc. Its ecological relations are those of *C. terglouensis* and *C. pygmaea*. It often grows with *Leontodon montanus*, which it resembles in habit. On the peak of the Pellinkopf it is found with *Taraxacum ceratophorum*; on Fimberjoch, with *Hieracium pumilum* and *Senecio Carniolicus*.

The species is monomorphic. The type specimen does not exist, but the problem of nomenclature has been so ably considered by Thellung (Vierteljahrsschr. Naturf. Ges. Zürich 68: 473–474. 1923) that a translation of his discussion must be given; it is as follows:

Crepis rhaetica, it is true, is not found in Hegetschweiler's herbarium; still, according to the diagnosis (published in 1840) and habitat ("below the pass between Val-Camogasco and Luvino on the Luvino side, 8000 ft. above sea level, with *Papaver pyrenaicum*, *Ranunculus rutaefolius*, and *Dianthus glacialis* [Pr. Heer!]"—hence, evidently, Lavirum Pass, where the plant more recently has been collected in abundance), there can be no doubt that its identity was with *C. jubata* Koch, which name was proposed 4 years later. If this fact has not hitherto been correctly discerned or not sufficiently appreciated, the reason lies in the existence of a homonymous but entirely different *C. rhaetica* (Froel.) Nyman, Consp. 2: 456. 1879, in syn. (= *Hieracium rhaeticum* Froel., Tirol

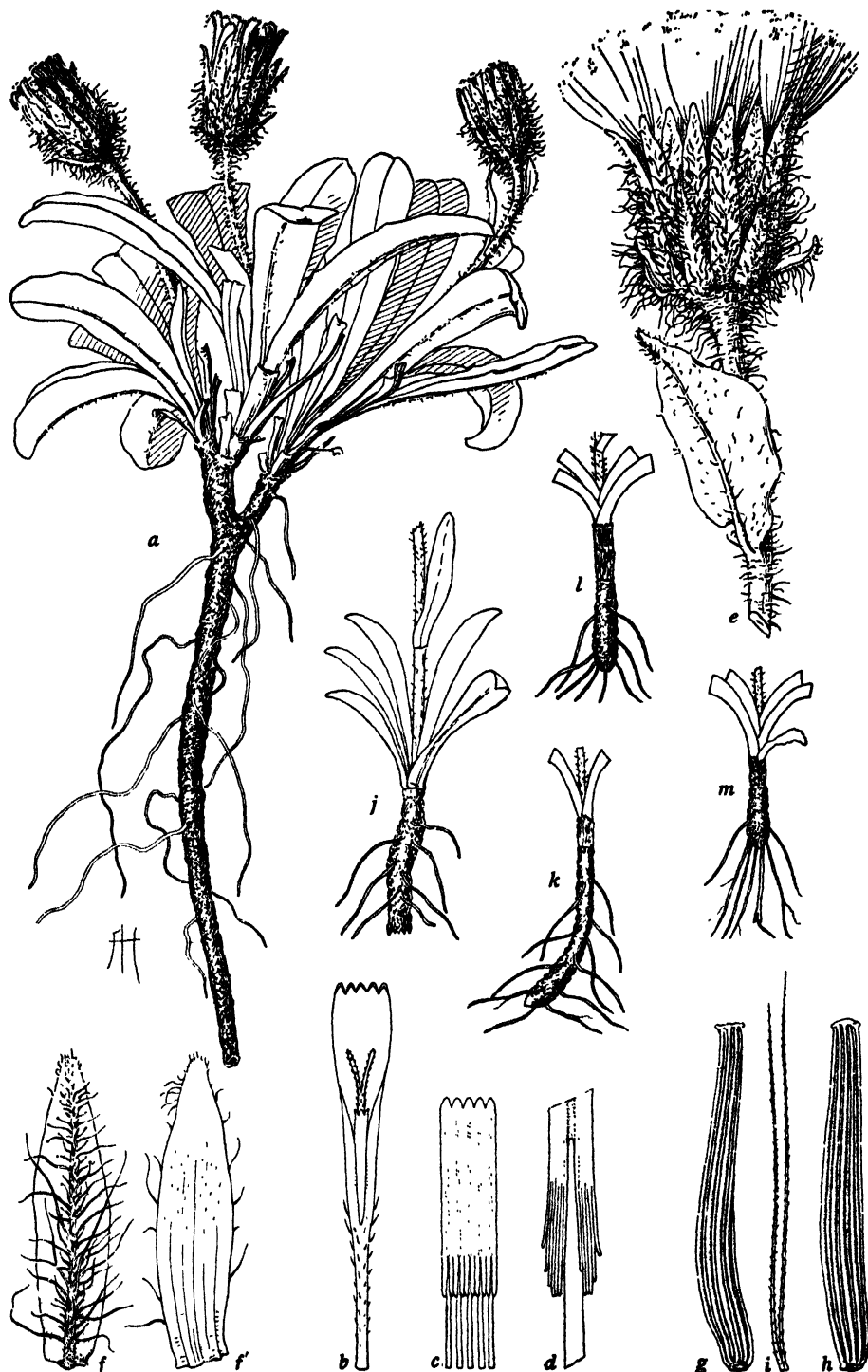


Fig. 24. *Crepis rhaetica*, a-d, from Käser in 1894 (Po 10539); e-f, from Lagge (Bo); g-j, from Käser in 1894 (UC 669413); k, l, from Huter (UC 452790); m, from Zimmer in 1879 (UC 669412): a, old, well-developed plant, $\times 1$; b, floret lacking ovary, $\times 4$; c, anther tube, $\times 8$; d, detail of appendages, $\times 32$; e, fruiting head and peduncle, $\times 2$; f, f', inner involucre bract, outer and inner face, $\times 4$; g-h, 2 achenes and a pair of pappus setae, $\times 8$; j, a much younger specimen in which the rhizome has been broken off, $\times 1$; k-m, still younger plants with praemorse rhizomes, $\times 1$. In k the apical region seems to indicate a potential downward extension of the rhizome.

Bote, 240. 1830, et ap. Rehb., Exeurs. 2: 260. 1831, hic in syn. ad *Geracium chondrilloides* var.; = *C. chondrilloides* var. *rhaetica* Froel., ex DC., Prod. 7: 171. 1838; = *C. Jacquini* var. *rhaetica* Beck, Fl. Nied.-Oesterr. II, 2: 1277. 1893), which appears to us as a form of *C. Jacquini* Tausch (*C. chondrilloides* [L.] Rehb., 1828 non Jacq., 1762), with which our *C. rhaetica* Hegetschw. was falsely identified by many authors (e.g., by Thellung in Schröter, Joh. Hegetschweiler, Neujahrsbl. Gelehrten Ges. Zürich 1913: 81, for want of an original specimen, on the basis of the position assigned by Hegetschweiler to his *C. rhaetica* directly after *C. "chondrilloides,"* i.e., *C. Jacquini*); whereas others (e.g., Bruegger, Schod. Herb. Helv. Eidg. Tech. Hochschule.), because of the mentioned homonym (*H. rhaeticum* Froel.), did not believe they were at liberty to use the name *C. rhaetica* in spite of its clearly admitted priority—a consideration which, according to modern rules of nomenclature, must be designated as inadmissible.

France: Savoie, Mt. Iseran, peak, *Bertrand et al.* in 1884 (Grenoble); *ibid.*, 2769 m, *Gillot* in 1893 (Bur). **Switzerland:** Valais, Chanrion, Brenny glacier, *Castella* (US); Valais, Bagnes Valley, near Lireroise glacier, *Tavrat* in 1883, *Pannatier* in 1902 (Bur); Engadin, Lavirum Pass, *Burnat* in 1873, *Candrian* in 1898 (Bur); *ibid.*, *Crettli* in 1875 (Bo); Engadin, Lasioun, *Davall* in 1853 (Bur); Engadine, between Sampiur and Samnaun, *Davall* ♀ in 1853 (Bur); Unter-Engadine, Samnaun Valley, west side of Valmatruga peaks, 2500 m, *Käser* in 1894 (Po, UC); Grisons, near Flims, north of Flimerstein, *Tavrat* in 1880 (Bur). **Italy:** near Zermatt, Hoernli, *Lagge* (Bur, Bo); *ibid.*, Hoernli peak, *J. Ball* in 1887 (US); central Tirol, Mt. Hühnerspiel, *Wagner* in 1879 (Minn); *ibid.*, Hühnerspiel am Brenner, in *Zimmer* in 1879 (UC); *ibid.*, Hühnerspiel, Gossensass, *Huter* 200 (Bur, US); central Tirol, Mt. Friedberg, *Huter* in 1887 (Bur, UC); central Tirol, Weisspitz, near Sterzing, *Huter* in 1900 (UC, Po, Minn).

Relationship

Crepis rhaetica, from its morphology and ovary anatomy, as well as its characteristically relic distribution, is a primitive species. On the basis of ovary anatomy it is just as primitive as *C. pygmaea* subsp. *anachoretica*, *C. kashmirica*, *C. geracioides*, and *C. sibirica*, since it has 4 or 5 supernumerary vascular strands in the ovary at anthesis (see Part I, appendix 4). In this respect it is a more primitive species than *C. terglouensis*. Although its achenes and their ribs are much narrower than those of *C. terglouensis* and *C. pygmaea*, the peculiar alternation of wider and narrower ribs (which is hardly noticeable unless the achenes are mature or nearly so) may be compared with the same peculiarity of *C. pygmaea anachoretica*; and in this respect, as well as its low-tufted habit, it shows affinity with *Youngia depressa* (cf. *C. pygmaea*). Unfortunately, it has not been possible to examine the chromosomes of *C. rhaetica*; but from the foregoing evidence they may be expected to resemble those of *C. terglouensis* in both number and form.

The most remarkable feature of this little-known relic species is its variability in rhizome length. In young plants the rhizome is short, vertical or oblique, and praemorse, with fleshy fibers (see fig. 24, *l, m*). In somewhat older plants, however, the rhizome, when not broken off by the collector, as in fig. 24, *j*, is definitely longer. Such an older plant with longer rhizome is shown in fig. 24, *k*. Furthermore, in some of these small, younger plants, in which the rhizome has not been damaged, the lower apex seems to have the appearance of being a region of active growth (see fig. 24, *k*). It is safe to assume that the more deeply penetrating rhizome of an old plant of this species has developed from a short rhizome. With respect to its underground parts, *C. rhaetica*, therefore, appears to be an intermediate species. But on the basis of other morphological characters, especially size and habit of the plant, size and shape of the leaves, the type of inflorescence, and the shape and ribbing of the achenes, this species is certainly closer to the other species of this section than to those of any other section.

9. *Crepis Jacquini* Tausch

Flora 11 (1 Erg.): 79. 1828. (Fig. 25.)

Perennial, 0.5–2.5 dm high; rhizome 1–5 cm long, dark brown, slender, oblique or vertical, strongly fibrous; caudex simple or divided; caudical leaves few or numerous, semierect, 3–15 cm long, 0.2–1.7 cm wide, oblanceolate to linear, acute, entire, remotely denticulate or dentate, runcinate-pinnatifid or pinnately parted with long terminal and remote narrow lateral lobes, gradually reduced into a narrowly winged petiole with broader base, glabrous, sparsely tomentulose or puberulent along midrib; cauline leaves similar or more narrowly lobed, gradually reduced upward, uppermost sometimes hirsute, like peduncles; stem erect, scapiform or cymosely branched above and 2–6-headed, terete, striate, canescent-tomentose, sometimes sparsely pubescent; branches pedunculate, 0.5–5 cm long, tomentose, sometimes hirsute, with green glandless hairs; heads medium, many-flowered; involucre cylindric-campanulate, 7–12 mm long, 4–8 mm wide at middle, canescent-tomentose, dark green and sparsely to densely hirsute, with green glandless hairs, or not hirsute and then sometimes pale green; outer bracts 6–10, unequal, longest $\frac{1}{2}$ – $\frac{2}{3}$ as long as inner bracts, linear, acuminate; inner bracts 12–16, in two or three unequal ranks, lanceolate, acute or obtuse, ciliate at apex, glabrous and strongly 2-nerved on inner face, nerves becoming indurate, otherwise little changed at maturity; receptacle areolate, glabrous; corolla about 13 mm long; ligule 1.5–2 mm wide; teeth 0.5–0.75 mm long; corolla tube 3.5 mm long, glabrous; anther tube 4.75–1.25 mm dis.; appendages 0.5 mm long, lanceolate, acuminate; filaments 1–1.25 mm longer; style branches 2–2.5 mm long, 0.1 mm wide, yellow; achenes light brown or stramineous, 4–5 mm long, 0.75–1 mm wide, straight or curved, \pm attenuate to both ends, \pm compressed or obcompressed or somewhat angled, 10–15(20)-ribbed, ribs rounded, smooth, or rugulose, sometimes very unequal, with 3–5 much stronger and thickened at the lightly calloused base; pappus cream, 7 mm long, 1–2-seriate, the setae nearly equal or very unequal in length and width, rather brittle, persistent. Flowers bright yellow. Chromosomes, $2n = 12$.

Hieracium chondrilloides L., Sp. Pl. 801. 1753 non Vill.

Crepis chondrilloides Rehb., ex Moesl., Handb. ed. 2, 2: 1403. 1828; Froel., ex DC., Prod. 7: 171. 1838 non Jacq.

Geracium chondrilloides Rehb., Fl. Germ. 260. 1830–1832.

C. Froelichii Steud., Nomencl. ed. 2, 436. 1840.

Aracium chondrilloides D. Diet., Syn. Pl. 4: 1330. 1839–1852.

Brachyderca chondrilloides Sch. Bip., ex Nym., Consp. 456. 1878.

Hieracioides chondrilloides O. Kuntze, Gen. 1: 345. 1891.

European Alps: From E. Switzerland eastward through Tirol and Bavaria to the Carpathian and Transylvanian Mts., and southward into Croatia, Dalmatia, and N.E. Albania. Subalpine and alpine, mostly between 1500 and 2800 m alt. Often in colonies on rocks and among loose rocks in the train of avalanches. Always on calcareous formations.

In Switzerland, acc. to Rübel (238), *C. Jacquini* occurs in "Alpen-matten" composed of *Carex firma*. In the W. Carpathian Mts., acc. to Pax (2: 152), this species occurs on the Chocs and other high peaks in the N. central region; but in contrast with its usual high elevations he also found it in Rajecz-Teplicz Valley, with other alpine plants, at about 370 m alt. In the E. Carpathians it occurs on rocks and cliffs of the highest peaks of Rodnaer Alps, Mt. Rareu, Mt. Ceahlau, and Burzenland Mts. (cf. Pax, 2: 200, 217). Pax lists it as a characteristic species of the alpine element in the Carpathians.



Fig. 25. *Crepis Jacquini*, a-g, from Jermy (US 369825); h, i, from Weber in 1935 (WSC 74226); j, from Engelhardt in 1929 (UC 463918); k, from Longa in 1898 (UC 669516); l, from hort. genet. Calif. 3467 (seeds from Tirol, received through Dr. F. v. Wettstein in 1938): a, plant, $\times 1$; b, floret lacking ovary, $\times 4$; b', detail of ligule tooth, $\times 50$; c, anther tube, $\times 8$; d, detail of appendages, $\times 32$; e, plant, $\times 1$; f, g, achene and a pappus seta, $\times 8$; h, i, flowering heads from two different plants in same collection in Czechoslovakia, $\times 2$; j, k, flowering heads from 2 different localities in Trentino, Italy, $\times 2$; l, somatic chromosomes, $n = 6$, $\times 1250$.

Although authentic specimens of Linnaeus and Tausch were not seen by me, numerous descriptions and illustrations are consistent with respect to identity and synonymy.

This species is highly variable in stature, size of heads, size and shape of leaves, and in nature and amount of indumentum. Based solely on presence or absence of dark green hairs on the involucre, 2 geographical races have been recognized by Hegi (1145), namely, var. *rhaetica* (Froel.) and var. *norica* (Froel.) DC. The former (with hairy involucre) occurs throughout the western part of the range and the latter is confined to the extreme eastern part. In middle Czechoslovakia both forms sometimes occur in the same collection of plants. Hegi also notes that the flower heads close toward midday.

Switzerland: Grisons, Engadine, *J. D. Hooker* in 1862 (K). **Italy:** Trentino, Alpes Lombardes, *Cornas* in 1884 (Bur); Sondrio, Bormio, *Longa* in 1911 (Bur); Tirol, Schlern, *Touton* in 1900 (UC); Tirol, Blaser Mt., *Obrist* 198 (K, US, G, Mu, Bur); Tirol, Bellimo, Mt. Siara, *Churchill* in 1872 (K). **Germany:** Bavaria, Oberammergau, Mt. Sonnenberg, *Lomax* in 1890 (UC); *ibid.*, *Follmann* in 1915 (Bur). **Austria:** (†) "Alp. Rhaetic," *Froelich* in 1827 (DC); Schunzburg, *Keller* in 1878 (UC); Styria, Mt. Natterriogl, Admont, *Steininger* in 1889 (UC). **Czechoslovakia:** Tatra Mts., *Jermy* (US); Bielské Tatry Mts., Javorinka Peak, *Domin et Deyl* in 1929 (UC, G, US); *ibid.*, Holubyho Valley, *Weber* in 1935 (WSC); S. Carpathian Mts., *J. Ball* (K). **Rumania:** Transylvania, "Alp. Trania," *Fronius* (UWG), as *Hieracium croaticum* Schur. **Albania:** Sala, above Bjeska maze, about 1900 m, *Dörfler* 257 (G).

Relationship

Although *Crepis Jacquini* shows considerable resemblance to *C. terglouensis*, it differs from that species in nearly every part of the plant and strikingly in important characters of the flowers and fruits. Yet natural hybrids have been reported in localities where the 2 species grow near each other (see $\times C. hybrida$ A. Kern.).

10. *Crepis hokkaidoensis* Babc.

Univ. Calif. Publ. Bot. 19: 400. 1941. (Fig. 26.)

Perennial, 1.5–2 dm high; rhizome vertical or oblique, elongated or praemorse, bearing fleshy fibers; caudex 0.5–1 cm wide, covered with the dark brown bases of old leaves; caudical leaves 6–14 cm long, 1–2.5 cm wide, oblanceolate or elliptic, sinuately or runcinately shallow-lobed or pinnatifid, the lobes close or remote, triangular or oblong acute, entire or 1-dentate, gradually attenuate into a narrowly winged petiole shorter than the blade, \pm pubescent on both sides and the margins with pale glandless hairs; cauline leaves 1 or 2, mostly 3–6 cm long, 0.5–2 cm wide, lanceolate, acute, sessile, amplexicaul-auriculate, pinnatifid, with narrow acute lobes; stems 1 or 2, 1-furcate, 2-headed, or scapiform, rather stout, terete, striate, fistulose, \pm tomentulose, pubescent toward summit, with long dark glandless hairs; peduncles 4–8 cm long, strict or arcuate, slightly dilated toward apex in fruit; heads erect, medium, about 40–50-flowered; involucre campanulate, 12–14 mm long, 10–12 mm wide at middle in fruit, dark brown in sic., canescent-tomentulose and densely pubescent, with fine brownish-green or pale mottled glandless hairs; outer bracts 6–10, unequal, longest $\frac{1}{2}$ – $\frac{2}{3}$ as long as the inner, lanceolate, acute, glabrous on inner face; inner bracts 10–20, in 2 ranks, inner ones wider, membranous at margin, lanceolate, acute, white-ciliate at apex, densely strigulose on inner face, with white, shining trichomes, becoming indurate and slightly thickened but otherwise unchanged at maturity; receptacle areolate, fimbriate, fimbriae low, shortly and finely ciliate; corolla about 19 mm long; ligule 1.75 mm wide; teeth about 0.4 mm long; corolla tube about 4 mm long, beset with short (0.5–1 mm long) stout trichomes; anther tube about 5 \times 1 mm dis.; appendages



Fig. 26. *Crepis hokkaidoensis*, a-i, from Tatewaki in 1921 (UC 346438); j-m, from Ishida in 1928 = hort. genet. Calif. 2747 (UC 429493): a, plant, $\times 1$; b, part of stem, with leaf and 2 heads, $\times 1$; c, d, outer, and e, f, inner involucre bracts, $\times 4$; g, floret lacking ovary, $\times 4$; g', detail of ligule tooth, $\times 25$; h, anther tube, $\times 16$; i, detail of appendages, $\times 32$; j-l, outer and inner achenes and pappus seta, $\times 8$; m, somatic chromosomes, $n = 4$, $\times 1250$.

about 0.5 mm long, acute; filaments 1.25 mm longer; style branches 2.75 mm long, 0.1 mm wide, dark brown in sic.; achenes dark brown, somewhat paler near summit, 7.5–10 mm long, 0.7–0.8 mm wide, gradually attenuate upward into a neck $\frac{1}{2}$ – $\frac{1}{3}$ as wide, with slightly expanded pappus disk, narrowed at the pale-calloused hollow base, about 20-ribbed, ribs weak, narrow, rounded, finely muriculate under lens; pappus dusky white, 5–7 mm long, 2–3-seriate, setae unequal in length and width, widest about 50μ (6 cells), rather stiff but pliable, very persistent. Flowering July–Aug.; flowers yellow. Chromosomes, $2n = 8$.

Crepis burejensis Miyabe et Miyake, Fl. Saghalin 284. 1915, non Fr. Schmidt.

Japan, on Mt. Yubari in Hokkaido; and, acc. to Miyabe and Miyake (*loc. cit.*), Rishiri Is., Kurile Is., Kokuruko Prov., and in Sakhalin. The authors mentioned state it occurs on exposed rocks of mountain peaks. Tatewaki (Acta Phytotax. Geobot. 2: 259. 1933) has reported this species from Kaiboto (Todomoshiri) I., southwest of Sakhalin, on Mt. Dainan and Gampizaka, in alpine meadows.

Monomorphic.

Hokkaido: Ishikari Prov., Mt. Yubari, *Ishida* in 1928, Aug. 23, fruits (UC ex Herb. Hokkaido Imp. Univ., Sapporo); *ibid.*, Mt. Yubari, gravelly slopes, *Tatewaki* in 1921, Aug. 3, flowers and fruits (UC ex herb. Kingo Miyabe); Yubaridake, 1600 m, *Uno 17204 (2596)* (G); Kabafuto, *Sugawara 812* (G).

Nomenclature

The confusion of this species with *C. burejensis* Fr. Schmidt, which appears to be a form of *C. chrysantha* (q.v.), is unfortunate because the present author has been unable to obtain a specimen of *C. burejensis* for examination. It is difficult to see how the mistake was made, however, since Schmidt's description of *C. burejensis* presents the following important differences:

C. burejensis (ex descr.)

plant 2–4 inches (5–10 cm) high
caudical leaves lanceolate-linear
stem scapiform, 1-headed
leaves glabrous or tomentulose
cauline leaves absent or 1, linear
heads about 30-flowered
achenes fusiform, 10-costate
habitat Bureja, E. Siberia

C. hokkaidoensis

plant 15–20 cm high*
caudical leaves oblanceolate or elliptic
stem 1-furcate, 2-headed or sometimes scapiform
leaves pubescent on both sides
cauline leaves 1 or 2, lanceolate
heads about 40–50-flowered
achenes oblong, attenuate upward, 20-ribbed
habitat Hokkaido, Japan

* Miyabe and Miyake (Fl. Saghalin 284. 1915) state 15–30 cm, but none of the 6 specimens sent to me by Professor Miyabe is over 20 cm high.

Relationship

Crepis hokkaidoensis is closest to *C. chrysantha* and *C. polytricha*, not only in gross morphology but also in karyotype; it is, however, very distinct from those species in the larger, pinnately lobed leaves, in the usually furcate stem, and especially in the many-ribbed achenes. The latter resemble those of *C. alpestris* in shape, but in number of ribs, as well as in shape, they are more like those of *C. sibirica*. In both leaf and achene characters this is a more primitive species than either *C. chrysantha* or *C. alpestris*. *C. hokkaidoensis* also shows considerable resemblance to *C. modocensis* in habit, involucre, and achenes, and, if not actually an ancestor of the latter, it probably represents one of the original stocks from which it was derived (cf. B. and S., 504: 31).

11. *Crepis aurea* (L.) Cass.

Diet. Sc. Nat. 25: 88. 1822; 27: 4. 1823. (Pl. 2. Fig. 27.)

Perennial, 0.2–3 dm high; rhizome slender, becoming praemorse, fibrous, swollen near the simple or furcate caudex; leaves all caudical, obovate or oblanceolate, dentate or pinnatifid, often mucronate, glabrous; stems 1–8, scapiform, sometimes furcate, rarely branched above, terete, striate, glabrous or hirsute above; heads erect, medium or rather large, many-flowered; involucre campanulate, dark green, hirsute, tomentulose or glabrous, little changed at maturity; outer bracts about 10, linear, unequal, longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as inner bracts, glabrous or hairy near base; inner bracts 12–16, oblong or lanceolate, narrowed toward the obtuse ciliate apex, ventrally glabrous; ligules yellow, orange, or reddish, and typically reddish-purple on the outer face; receptacle areolate or alveolate, with few or many white trichomes 0.1–0.2 mm long; achenes pale brown, subterete, fusiform, rather strongly attenuate upward to the slightly expanded pappus disk, with a small basal callus and about 16 fine smooth or spiculate ribs; pappus exceeding the involucre, white, soft, fine, rather persistent. Flowering July–Sept.

Alps of E. France, Switzerland, S. Germany, Austria, and N. Italy; the Apennines; mountains of W. Balkan Pen. south to N. Greece; N.W. Asia Minor; in alpine or subalpine meadows.

This well-known species is highly variable even within restricted regions in response to local environmental differences. Based on the types of Cassini and Tenore, 2 subspecies are recognized, which are connected by many intergrading forms, some of which are listed below as numbered variants.

Key to the Subspecies of Crepis aurea

Heads larger; involucre about 10 mm long; florets about 16 mm long 11, *a. typica*
Heads smaller; involucre about 7 mm long; florets about 11 mm long 11, *b. lucida*

11, *a. Crepis aurea typica* (Fiori) Babe., Univ. Calif. Publ. Bot. 19: 399. 1941. Plant 1–3 dm high; leaves rosulate, obovate or oblanceolate; stems 1–4 (5) (6), like the involucre \pm hirsute and with 1 or 2 small bracts; involucre about 10 mm high, densely covered with long and short dark green glandless hairs; inner bracts 13–16; florets about 16 mm long; ligule 2 mm wide, deep orange or orange-yellow and reddish dorsally; corolla tube about 6 mm long, shortly pubescent; anther tube about 5.25×1.25 mm dis.; appendages about 1 mm long; filaments 1 mm longer; style branches 1.4–2 mm long, green; achenes about 6 mm long; pappus 6 mm long. Chromosomes $2n = 10$. See pl. 2, *a* and fig. 27, *a–f*.

Leontodon aureus L., Syst. ed. 10, 1193. 1758–1759.

Hieracium aureum Scop., Carn. ed. c, 2: 104. 1772.

Calliopea aurea Don, Edinb. N. Phil. Journ. 1828–1829. 309.

Geracium aureum Rehb., Fl. Germ. Excurs. 259. 1830–1832.

Crepis Kitaibelii Froel., ex DC., Prod. 7: 168. 1838.

Brachydera aurea Sch. Bip., Pollichia 22–24: 318. 1866.

Hieraciodes aureum O. Kuntze, Gen. 1: 345. 1891.

Crepis aurea a. typica Fiori, Fl. Anal. Ital. 3(2): 441. 1904.

France and eastward throughout the Balkan regions into N. Asia Minor; subalpine and alpine meadows. Acc. to Braun-Blanquet and Rübel (1482), it ranges from 900 to 2790 m alt. in the middle E. Swiss Alps, mostly on neutral or weakly acid soils, especially in the *Festuca violacea*–*Trifolium Thalii* association.

Type locality unknown. In lieu of an authentic specimen antedating publication of the species by Cassini, the plant in Herb. Kew, seen by Cassini and bearing the

annotation, *Hoppe misit Aprili, 1823*, is accepted as the type. The locality given for this specimen, *in alpe Posteze (?)*, is unknown to me. The following note, attached to this specimen, is good evidence of the authenticity of the specimen :

"Je n'ai point ... le paquet l'*Hieracium aureum* (Villars), dont Linné faisait un *Leontodon*, et Scopoli une *Andryala*. L'ayant vu au jardin du roi, avant la fleuraison, je jugai, par ses feuilles, ... etc., probablement un *Crepis*; et quand il fut fleuri, je vivifiaï facilement que un conjecture était exacte. C'est pourquoi je l'ai décrite, sous le nom de *Crepis aurea*, dans le Dict., tom. 27, p. 4." This is followed by a subscript in different handwriting, *H. Cass. Decembre, 1826*.

Reduced forms are frequent. They usually have the hairy involucre and deeply colored ligules of *typica* and are not to be confused with other forms which are

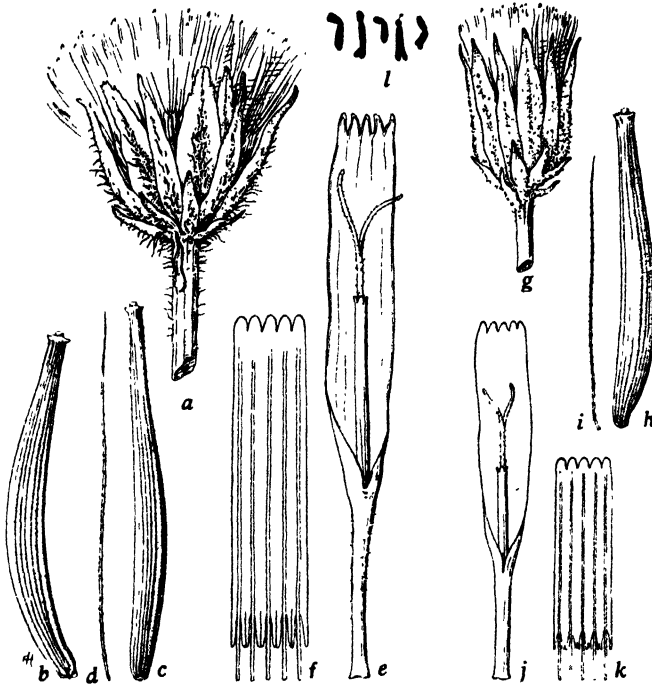


Fig. 27. *Crepis aurea typica*, a-f, from type (K) ; l, from hort. genet. Calif. 2170 (seeds received from Copenhagen Bot. Gard.) : a, mature head (in packet with type), $\times 2$; b-d, achenes and pappus seta, $\times 8$; e, floret lacking ovary, $\times 4$; f, anther tube, $\times 8$; l, somatic chromosomes, $n = 5$, $\times 1250$.

C. aurea lucida, g-k, from specimens of *H. Groves* (K) (cf. pl. 2, d, upper right) : g, mature head, $\times 2$; h, i, achene and pappus seta, $\times 8$; j, floret lacking ovary, $\times 4$; k, anther tube, $\times 8$.

intergradient between the 2 subspecies in other characters as well as size of plant (see numbered variants).

France: Alta Sabaudia, *Bouchard* (DS) ; Hautes-Alpes, Mt. Goudron near Briançon, *Sieber* in 1829 (K) ; Hautes-Alpes, Lauteret, *Pellat 1715* (K, Bur) ; Haute Savoie, Mt. Vergy, *Bourgeau* in 1873 (Ms) ; Savoie, Mt. Nivolet a la Gornaz, near Chambéry, *Huguenin 409* (Ms, K, Bur) ; loc. ?, *Villars* in Herb. Willd. n. 14635 fol. 5 (BW). **Switzerland:** Verne, *Mouillefarine* (Po) ; Valais, glacier of the Rhone, *Burnat et al.*, in 1915 (Bur) ; Hautes-Alpes, Montgenevre, near Mt. Goudron, *Lanner* in 1879 (K) ; Grisons, Engadine Valley, *J. D. Hooker* in 1862 (K) ; Bern, summit of the Fathhorn, *Martins and Bravais* in 1841 (K). **Italy:** Venetia, Belluno Prov., St. Vito del Cadore, *Pampanini and Minio* in 1908 (K, Bur). **Germany:** Bavaria, Berchtesgaden, *Einsele* in 1847 (K) ; Pfronten, Falkenstein, *Zick* in 1903 (Bur). **Austria:** Carinthian Alps, near Heblut, *Hoppe* in 1832 (DC) ; Haute-Sutriche, Windischgarsten, *Voselmann* in 1871 (Bur) ; Tirol, *Huter* in 1865 (K) ; Tirol, Madonna di Campiglio, *Woronin* in 1892 (Lenin) ; Austrian littoral (Din-aric ?) Alps, *Tommasini* (G). **Balkan Pen.:** Croatia, Alps, Herb. Willd. n. 14635, fol. 4 (BW) ; Croatia, Mt. Visocica, near Pocitely, *Degen* in 1906 (K) ; Croatia, Velebit, near Medak, *Degen* in

1905 (Bur, Fl, Ms, Sydney); Croatia, Velebit, Pociteljaka Draga, *Lengyel* in 1909 (US) m.v. 6; Croatia, Velebit Stirovacka Pojana, *Degen* in 1909 (UC) m.v. 6; Hercegovina, Trebinje dist., Mt. Prasa, *Vandas* in 1891 (K) m.v. 2; Albania, *Baldacci* in 1897 (Fl) m.v. 3; Albania, Mt. Parum, Scutari dist., *Baldacci* in 1897 (K) m.v. 5. Asia Minor: Bithynia Olympus, northern slope, *Pichler* in 1874 (K) m.v. 3.

Minor Variants of C. aurea typica

2. Similar to this subspecies, but smaller in all parts of the plant. *Vandas* in 1891 (K) Mt. Prasa, Hercegovina.

3. (*C. olympica* C. Koch, *Linnaea* 23: 691. 1850.) Like subsp. *typica* in stature, length of involucre and style branches, and in indumentum, but in habit and leaf shape it resembles subsp. *lucida*. *Pichler* in 1874 (K) Olympus Bithynicus, Anatolia; *Baldacci* in 1897 (K) Mt. Parum, Scutari dist., N. Albania.

5. Resembles this subspecies except the pinnatifid leaves. *Baldacci* in 1897 (Fl) Albania.

6. (*C. Kitaibelii* Froel., ex DC., *Prod.* 7: 168. 1838.) Like subsp. *typica* on the basis of size, but resembles subsp. *lucida* in slenderness, the glabrescent involucre, and the pale flower color. *Kitaibel* (DC. *Prod.* vii. 168 no. 37) Croatian Alps; *Lengyel* in 1909 (US) Croatia; *Degen* in 1909 (UC) Croatia.

11, *b. Crepis aurea lucida* (Ten.) Bab., Univ. Calif. Publ. Bot. 19: 399. 1941. Plant 0.2–1.6 dm high; leaves rosulate, oblanceolate; stems 1–8, like the involucre glabrous or sparsely canescent-tomentulose and with 1 or more minute bracts; involucre about 7 mm high, glabrous or sparsely tomentulose; inner bracts 12–15; florets about 11 mm long; ligule 1.75 mm wide, deep yellow, with or without a red dorsal median stripe; corolla tube 3–4 mm long, glabrous or shortly pubescent; anther tube about 3 × 1 mm dis.; appendages 0.5 mm long; filaments 1 mm longer; style branches 1.25 mm long, green; achenes about 5 mm long; pappus 4–4.5 mm long. Chromosomes, $2n = 10$. See pl. 2, *b* and fig. 27, *g–k*.

Apargia lucida Ten., Fl. Neap. 2: 164. 1820.

Hieracium columnae Ten., Syll. 398. 1826.

Hieracium pumilum Ten., Viagg. Cal. 128. 1827, *Prod.* 5: 25. 1835–1836, non Hoppe.

Crepis crocea Rchb., ex Moesl., *Handb.* ed. 3, 2: 1465. 1833.

C. columnae Froel., ex DC., *Prod.* 7: 167. 1838.

C. Sartoriana Boiss. et Heldr., *Diag. Pl. Or. Nov.* ser. 2, 3: 100. 1856.

Italy and the Balkan reg.; mountain meadows.

Type locality unknown. Type in Herb. Kew, *Apargia lucida*, with the following annotation, *Tenore dedit, Sept., 1824*. On the same sheet is a similar but larger plant labeled *Hieracium pumilum* Ten! = *H. columnae* c., Ten! with annotation, *Tenore misit, Feb. 1827*. Variable in size of plant and leaf shape but characteristically dwarf, slender, and glabrous. Occasional variants have the involucre ± pubescent (see minor variants).

Italy: Campania, Neapolitana, Aprutia, Majella Mts., *Porto and Rigo* in 1874 (Bur); Aprutia, Majella Mts., above Caramanico, *Huet* in 1856 (K, G); Mt. Meta, *Levier* in 1872 (Bur, BML); Etruria, Pistoilse Apennines, *Sommier* in 1882 (Bur); Bonnonian Apennines, *J. Ball* in 1844 (K); Lucania, Mt. Cervati, *Lacaita 229/14* (BML); Calabria Citra, Mt. Mula, *Lacaita 432/12* (BML); Apennines, Pisana dist., *Savi* (G); Etruria, Firenze Prov., Bascolungo, *Fiori et Béguinot* in 1917 (K, BML, Co) m.v. 1; Italy (†) ex *Gussone* in 1828, 1831, and ex *Tenore* in 1833 (DC) m.v. 1. **Balkan Pen.:** Albania, Epirotica, Kakarditze Tsumerka Mts., *Baldacci* 169 (K, Bur); Montenegro, Ledenic plain, *Rohlena* in 1905 (BML); Montenegro, Mt. Kunj Kostic, Kuci dist., *Baldacci* 135 (K, Bur) m.v. 4; Crneagora (†) *Baldacci* in 1891 (K) m.v. 4; (†) Acquanian Alps, *J. Ball* in 1866 (K) m.v. 4; Hercegovina, Mt. Kom, *Pantocsek* in 1872 (Bur); Hercegovina, Trebinje dist., Mt. Prasa, *Vandas* in 1891 (K) m.v. 5; N. Greece, Eurytania, Mt. Veluchi, *Heldreich* in 1879 (K, Bur, Ms); Greece, Zygos Mts., Morava Peak, north slope, *Babcock* 352 (UC) m.v. 7; Greece, Arcadia, Mt. Olenos, *Heldreich* in 1848 (K, G); Greece, Thessaly, Mt. Ossa, *Miss Topali* 38–12 (UC).

Minor Variants of C. aurea lucida

1. (*C. aurea* var. *lucida* Grande, Bull. Ort. Bot. Napoli 5: 58. 1918; *C. aurea* B. *columnae* c. *hispidula* Fiori, Fl. Anal. It. 3: 442. 1904.) Actually an intergrade, with tall, slender stems, long, narrow leaves, rather small heads, and hirsute involucres. *Fiori et Béguinot* in 1917 (K, BML, Co) Bascolungo, Etruria, Italy.

4. Resembles this subspecies, but has long black hairs on the involucre and tomentum on the peduncle. *Baldacci* 185 (K, Bur) Mt. Kunj Kostic, Kuci dist., Montenegro.

7. Involucre pubescent and, like peduncle, canescent-tomentulose; ligules with or without red dorsal stripe; style branches 1.5 mm long. *Babcock* 352 (UC) abundant in sod, steep meadow, north slope of Morava Peak, Zygos Mts., N. Greece.

Relationship

In its karyotype this species is closer to *Crepis albida* than to the more primitive species of this and preceding sections. But its chromosomes also suggest that it may have sprung from the same primitive stock as *C. tingitana* (q.v.) and *C. leontodontoides*. Furthermore, cytological evidence (see Avery, 154–156) certainly indicates a sufficient degree of genic homology between *C. aurea* and *C. leontodontoides* to cause high meiotic regularity in hybrids between the 2 species. *C. aurea*, or some related 10-chromosome species, may have figured in the ancestry of the somewhat similar 8-chromosome species, *C. chrysanthia*. In gross morphology it also shows resemblance to *C. Jacquinii* and *C. terglouensis*. But *C. aurea* must be considered as a rather advanced member of the section, with no very closely related species in the section.

12. *Crepis chrysanthia* (Ledeb.) Froel.

Ex DC., Prod. 7: 165. 1838. (Pl. 3. Fig. 28.)

Perennial, 0.8–2 dm high; rhizome vertical or oblique, 2–3 cm long, slender, becoming praemorse, fibrous; caudex covered with brown bases of old leaves, simple or furcate; caudical leaves erect or ascending, up to 9 cm long, 2 cm wide, oblanceolate, obtuse or acute, sinuate-dentate or denticulate, gradually attenuate into the narrow petiole, with broader clasping base, sparsely or densely canescent-tomentulose or glabrescent; cauline leaves 1–3, remote, lowest similar to caudical leaves or sessile, the others linear or bractlike; stem or stems simple, scapiform, or sometimes 1–3-furcate with pedunculate branches, terete, striate or sulcate, fistulose, becoming notably thickened near head, glabrous below, pubescent above, with dark green glandless hairs becoming longer and denser near head; head erect, rather large, many-flowered; involucre (10, 12) 14–16 mm high, campanulate, densely hirsute, with dark green glandless hairs, not thickened at maturity, ultimately reflexed; outer bracts 10–15, sometimes with several similar subtending ones, unequal, longest $\frac{2}{3}$ as long as inner bracts, oblong or lanceolate, obtuse or acute; inner bracts 15–18, lanceolate, acute, canescent-tomentose at apex, silky-pubescent on inner face; receptacle areolate-fimbriate, fimbriae low, densely white-ciliate; corolla in marginal florets 13–19 mm long; ligule 2.5 mm wide; teeth 0.3–0.4 mm long; corolla tube 4–6 mm long, sparsely beset with papilliform hairs up to 0.2 mm long; anther tube 5.5×1.25 mm dis.; appendages 1 mm long, narrow, acuminate; filaments 1 mm longer; style branches 2.5 mm long, 0.15 mm wide, yellow; achenes reddish-brown or dark purple, 5–7 (9.5) mm long, straight or somewhat curved, subterete, fusiform, usually more definitely attenuate toward summit than base, sometimes strongly attenuate and paler at summit, slightly constricted above the pale-calloused hollow base, 15-ribbed, ribs equal or sometimes 3 or 4 stronger ones, rounded, obscurely rugulose or finely spiculate near apex; pappus white, 5–7 (8) mm long, 2-seriate, the setae unequal, 30–65 μ wide at base, rather soft, persistent. Flowering July–Sept.; flowers yellow. Chromosomes, $2n = 8$.

Hieracium chrysanthum Ledeb., Fl. Alt. 4: 129. 1833.

H. frigidum Steven, ex DC., Prod. 7: 165. 1838.

H. frigidum Turcz., pl. exsicc. 1829, ex Ledeb., Fl. Ros. 2: 826. 1844–1846.

Berinia chrysanthia Sch. Bip., Pollichia 22–24: 319. 1866.

Crepis burejensis Fr. Schmidt, Mem. Acad. Imp. Sci. St. Petersburg. 12(2): 52. 1868.

Hieraciodes chrysanthum O. Kuntze, Gen. 1: 345. 1891; non *C. chrysanthia* Koch = *C. rhaetica*.

Arctic Eurasia and the alpine zone in mountains of N. Asia from the Ural Mts. eastward to Kamchatka. According to Hulten (F. Kamchatka 8[2] : 231. 1930) the geographical area is as follows: Europe—E. Samoied Land and in Perm Prov. and Orenburg Prov. of the Urals. Asia—from Ob Gulf, Novil Mts., lower Lena R., and Chukch Pen. southward in the mountains to Altai, Sayan Range, N. Mongolia, Transbaikalia, Yakutsk, and S. Kamchatka. Komerov (Fl. Pen. Kam. 3 : 204. 1930) gives the following on habitat in Kamchatka: alpine meadows among stones, on alpine moist, rocky plains, and on the products of volcanic eruptions. Also, according to Hulten, occasionally found in the lowlands among washed-down material of the rivers. With a fragmentary specimen collected by Miss Tjulina on Mt. Teremel in the S. Ural reg. was the notation, "in lichenous tundra."

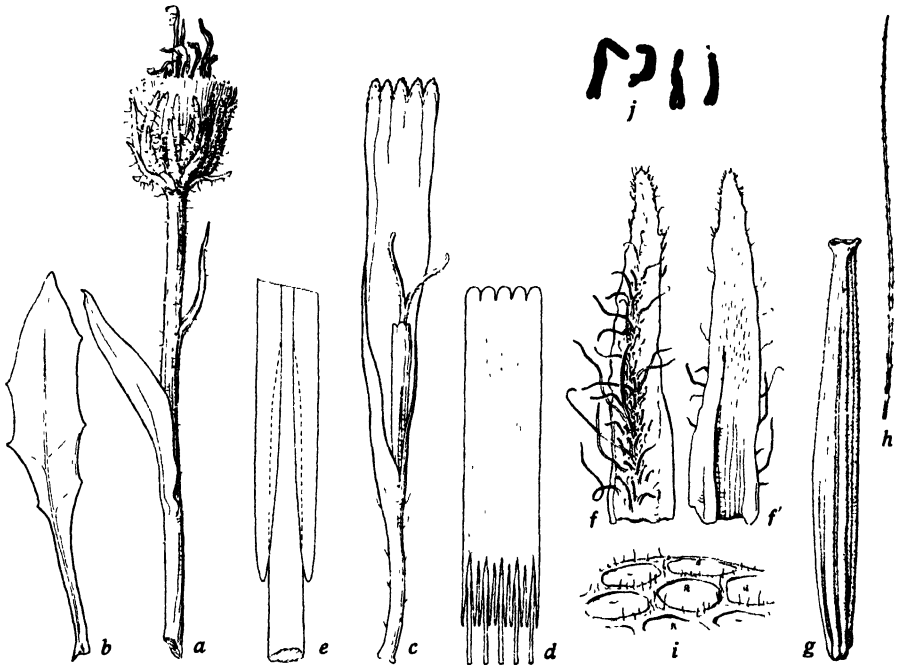


Fig. 28. *Crepis chrysantha*, a-f, from a typical spec. (Bo); g, h, from Turczaninow in 1829 (DC); i, from Tjulina in 1929 (UC 660567); j, from hort. genet. Calif. 2179 (seeds received from Mongolia through Dr. M. Navashin): a, stem and head, $\times 1$; b, caudical leaf, $\times 1$; c, floret lacking ovary, $\times 4$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, f', inner involucre bract, outer and inner face, $\times 4$; g, h, achene and a pappus seta, $\times 8$; i, detail of receptacle, $\times ca. 15$; j, somatic chromosomes, $n = 4$, $\times 1250$.

This widely distributed species is very scantily represented in herbaria outside of Russia. A number of varieties and forms have been named by Russian botanists, but, because the specimens involved have not been seen by the present author, they will not be listed here. The above description is based on specimens in the de Candolle and Boissier Herbaria compared with specimens seen at Berlin, Vienna, and Florence, and some borrowed from the University of Moscow and the U.S. National and Gray Herbaria. The specimens in the de Candolle Herbarium were considered authentic, and they include 2 forms which have been named as varieties. Ledebour (*loc. cit.*) gives a meager description of var. *tubaeformis* (= *H. frigidum* Turcz., pl. exsic. 1829), and Herder (199) lists a form collected in the Altai by Ledebour as var. *genuina*. Specimens from both of these collections (see pl. 3), together with one of Bunge's, also collected in the Altai, comprise the critical material in Herb. DC.

Prod. 7: 165, n. 28. They all certainly belong to this species, the annotation of J. Muller, 1853, to the contrary notwithstanding.

Most of the named varieties and forms referred to above are based on differences in size of plant, degree of dissection of the leaves, or variations in the indumentum. Of greater importance are the marked variations in size and shape of the achenes which have been noted by the author, even among the few available fruiting specimens. But, as most of the observed differences in size and shape of achenes have been found in a single accession of seed from Mongolia, it is inferred that these differences are not restricted to certain geographic races, but, rather, that the species as a whole is variable in this respect. It should be noted that the var. *polytricha* Herder (*op. cit.*, 200) is *C. polytricha* Turcz., a distinct species (*q.v.*).

Russia: S. Ural Mts., Mt. Teremel, in lichenous tundra, *Miss Tjulina* in 1929 (UCf). **N. Central Asia:** Kumak R., *Nilsson* in 1898 (Hayek). **Siberia:** Altai, ex Acad. Petropol. 1835 (DC, B); Altai, "Tigeretskij bjelor," *Titov* in 1913 (G); E. Altai reg., *Bunge* (DC, G); Irkutsk, Sajon Mts., sources of the Irkut R. and Oka R., *Komarov* in 1902 (B); Baikal reg., alps of Schibet and Urgude, *Turczaninow* in 1829 (DC, Bo, K, B, G, UCf); W. Baikal reg., *Turczaninow* (K, US); Kamchatka Pen., 1060 m, *Koslovskij* 1435 (B); Kamchatka, Korjatakaja Volcano, *Eyerdam* in 1928 (G). **Mongolia:** Tyrelsch R. basin, exposed summit of Mt. Bain-Barat, *Kondratieva* 63 (Mose); Outer Mongolia, Chan-gui (Khangai) Mts., small swamps, summit of Mt. Han-Undur-ul, source of Hoitu-Tamir R., *Pavlov* 1361 (Mose, NY); *ibid.*, summit of Mt. Boro-Urgo, grassy flats, *Pavlov* 1498a (Mose).

Minor Variant of *C. chrysantha*

1. (*C. burejensis* Fr. Schmidt, Mem. Acad. Imp. Sci. St. Petersburg. 12[2]: 52. 1868; *Berimia chrysantha* Sch. Bip. b. *runcinata* Ledeb., *fide* Herder, Bull. Soc. Nat. Mosc. 43: 199. 1870.) Acc. to Schmidt (*loc. cit.*), stems only 0.5–1 dm high and slender; caudical leaves profoundly runcinate-pinnatifid. Otherwise Schmidt's description agrees perfectly with *C. chrysantha* and hence this is apparently merely a reduced form of *C. chrysantha*. This opinion is corroborated by Herder (*loc. cit.*), who found similar plants among Radde's collections in the Czokondo Mts., and in Dauren, Manchuria. *Bureja* is in Amur Prov., E. Siberia. Thus, the distribution of *C. burejensis* is included within the range of *C. chrysantha*. It became necessary to give special attention to this form because of its confusion with *C. hokkaidoensis* (*q.v.*). Although no specimens could be obtained for examination, the inclusion of *C. burejensis* under *C. chrysantha* appears to be wholly warranted.

Relationship

Crepis chrysantha is close to *C. polytricha*, from which it is easily distinguished by the smaller, cylindric-campanulate heads and green indumentum of the involucre, the generally more attenuate achenes, narrower anther tube appendages, and shorter corolla, as well as by the chromosome number which is 8 instead of 16. It may be the progenitor of *C. polytricha* (*q.v.*); and it certainly is related to *C. Bungei* (*q.v.*). Next in order of similarity stand *C. aurea* and *C. Jacquini*; but these have 5 and 6 pairs of chromosomes, respectively, and in this respect are more primitive, even though now restricted to mountains of S. Europe.

13. *Crepis polytricha* (Ledeb.) Turcz.

Bull. Soc. Nat. Mosc. (1838) 96; 21(2): 113. 1848. (Fig. 29.)

Perennial, 1.2–1.4 dm high; rhizome vertical, slender, covered above with brown bases of old leaves; caudex simple, or furcate; caudical leaves erect or ascending, up to 8 cm long, 1 cm wide, acute, sinuate-dentate, runcinate or pinnatifid, gradually attenuate into the short or long narrow petiole, with broader clasping base, villous, with white glandless hairs; cauline leaves 1 or 2 or absent, when present the lower one about midway between base and head, sessile, lanceolate, acute, with swollen dentate or lacinate base, upper one near head, bractlike; stem simple, scapiform, terete, sulcate with pale ridges, fistulose, becoming notably thickened near head, villous below, setuliferous above, with greenish-yellow glandless hairs be-

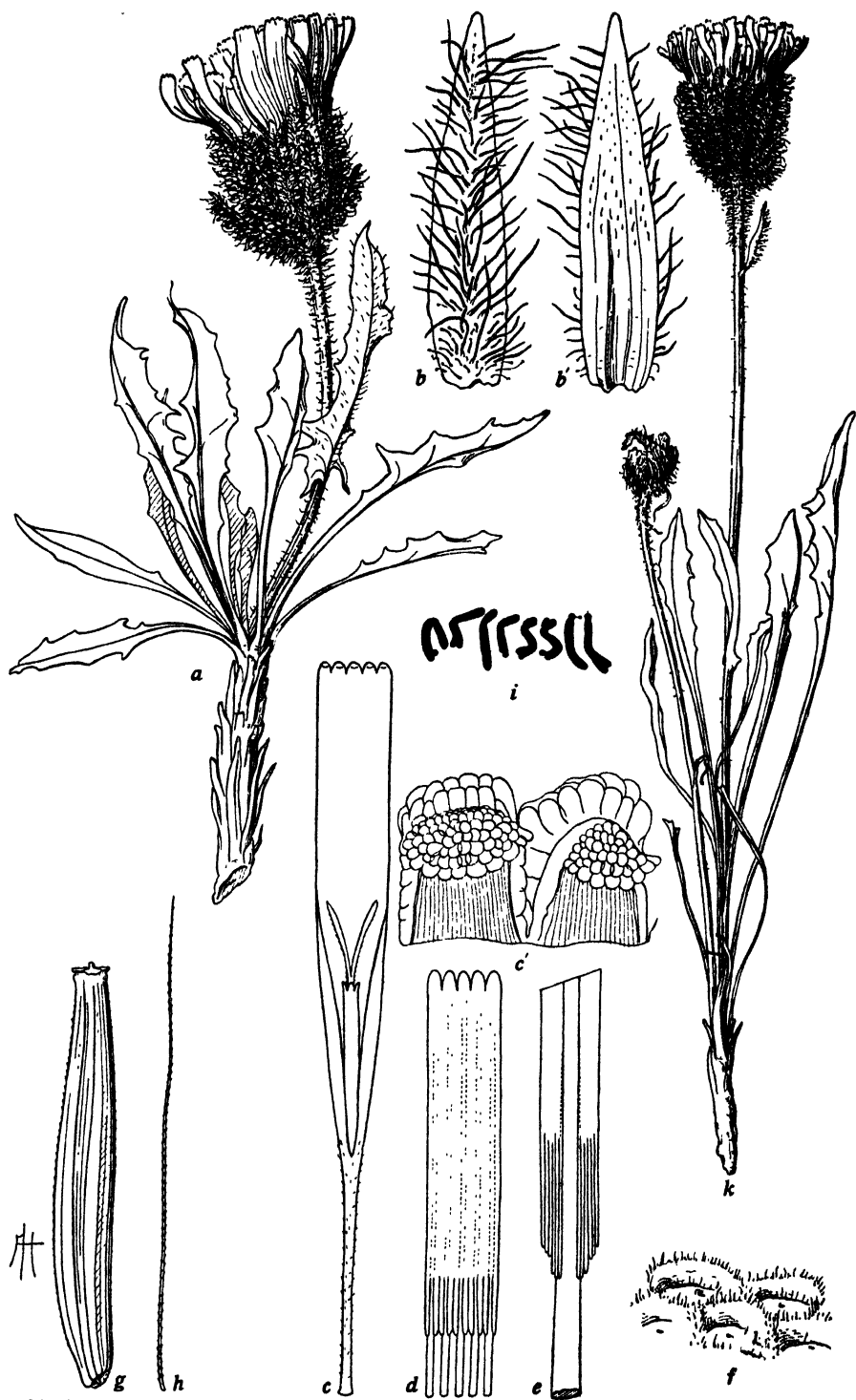


Fig. 29. *Crepis polytricha*, a-e, from isotype (Bo); f-i, from Schischkin in 1927 (UC 499376, seeds as hort. genet. Calif. 2562); k, from Pavlov 1498b (Mosc): a, plant, $\times 1$; b, b', inner involucre bract, outer and inner face, $\times 4$; c, floret lacking ovary, $\times 4$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, detail of receptacle, $\times 25$; g, h, achene and a pappus seta, $\times 8$; i, somatic chromosomes, $n = 8$ ($x = 4$), $\times 1250$; k, plant, $\times 1$.

coming longer and denser near head; head erect, large, many-flowered; involucre campanulate, about 15 mm high, 10 mm wide at middle, like peduncle canescent-tomentose at base, densely hirsute, with long crinkled glandless greenish-yellow hairs and shorter green glandular hairs especially near base and margins of bracts, becoming indurate but not much changed at maturity; outer bracts 8–10, unequal, $\frac{1}{2}$ – $\frac{2}{3}$ as long as inner ones, lanceolate, acute, becoming lax or partly reflexed; inner bracts 15–18, in two ranks, innermost scarious-margined, lanceolate, acute, canescent-tomentose at apex, silky-pubescent on inner face; receptacle alveolate, fimbriae 0.1–0.3 mm high, margins very shortly and finely ciliate; corolla in marginal florets 18–25 mm long; ligule 2.5–3 mm wide; ligule teeth 0.25–0.4 mm long, obtuse or truncate; corolla tube 5–8 mm long, slender, beset from base to summit with very short (up to 0.1 mm long) papilliform hairs, or with a few papilliform hairs up to 0.2 mm long, or glabrous; anther tube (5.75) 6.25 \times 1.25 mm dis.; appendages 1 mm long, oblong, obliquely acute; filaments 1 mm longer; style branches 2.5–3 mm long, 0.15–0.25 mm wide, attenuate, yellow; achenes dark purplish, 7 mm long, 1 mm wide at middle, 0.5 mm wide at summit, subterete, fusiform, gradually attenuate upward, slightly constricted below the narrow yellow pappus disk, constricted above the narrow oblique yellow-calloused base, about 20-ribbed, ribs narrow, nearly equal or 2 or 3 stronger, rounded, finely spiculate under lens; pappus white, 8 mm long, 2-seriate, rather coarse, soft, persistent. Flowering July–Aug.; flowers yellow. Chromosomes, $2n = 16$.

Hieracium polytrichum Ledeb., Fl. Alt. 4: 130. 1833.

H. alpinum var. *polytrichum* DC., Prod. 7: 209. 1838.

H. runcinatum Turcz., pl. exsic. 1832 ex Ledeb., Fl. Ros. 2: 827. 1844–1846.

Berinia polytricha Sch. Bip., Pollichia 22–24: 317. 1866.

Berinia chrysantha var. *polytricha* Herder, Bull. Soc. Nat. Mosc. 43: 200. 1870.

Mountains of N. Central Asia from the Altai to Transbaikalia; alpine. This little-known species is apparently rare, as it occurs in the same region and sometimes at the same locality as *C. chrysantha*, but has been collected only a few times. Turczaninow states that he did not see it elsewhere than at the type locality.

Monomorphic.

Siberia: *Dahuria* (= Transbaikalia), Czokondo Alps, Turczaninow in 1832 (Bo, K) isotypes; Altai reg., peak of Mt. Jete, 2000 m, alpine, Schischkin in 1927 (UC); Altai, Tschuja R. (fide Ledeb., loc. cit.); Altai, source of Dshelo R., Krylov in 1901 (NY). **Outer Mongolia:** Chan-gai (= Khangai) Mts., summit of Mt. Boro-Urgo, grassy flats, Pavlov 1498b (Mosc).

Relationship

Obviously closely related to *Crepis chrysantha*, *C. polytricha* is easily distinguished from the former species by the larger, ventricose involucre, with its yellowish indumentum. The corolla is also larger in *C. polytricha*, the anther tube longer, the appendages broader and obliquely acute, and the style branches broader. Furthermore, *C. polytricha* has 16 instead of 8 chromosomes. Critical study of its chromosomes was very difficult because of the small amount of material available and the close, overlapping arrangement of the chromosomes in the few mitotic figures found. It is not unlikely that *C. polytricha* originated as an amphidiploid hybrid between *C. chrysantha* and some other 4-paired species.

14. *Crepis albiflora* Bab.

Univ. Calif. Publ. Bot. 19: 399. 1941. (Fig. 30.)

Perennial, 0.6–1.2 dm high; rhizome short, vertical, praemorse, fibrous, about 1 cm wide at the simple crown or caudex; leaves all caudical, 2–5 cm long, 1–2 cm wide, oblanceolate, acute, pinnately parted, lobes narrow, oblong or lanceolate,

acute, dentate, \pm salient, petiole alate, dentate, broader and scarious toward base, glandular pubescent, hairs very short, fine, pale, glands very small, white; stems 1 or 2 (or more under cultivation), scapiform, simple, or 1-furcate, striate; peduncles gland-pubescent; heads erect, medium, 20–30-flowered; involucre cam-

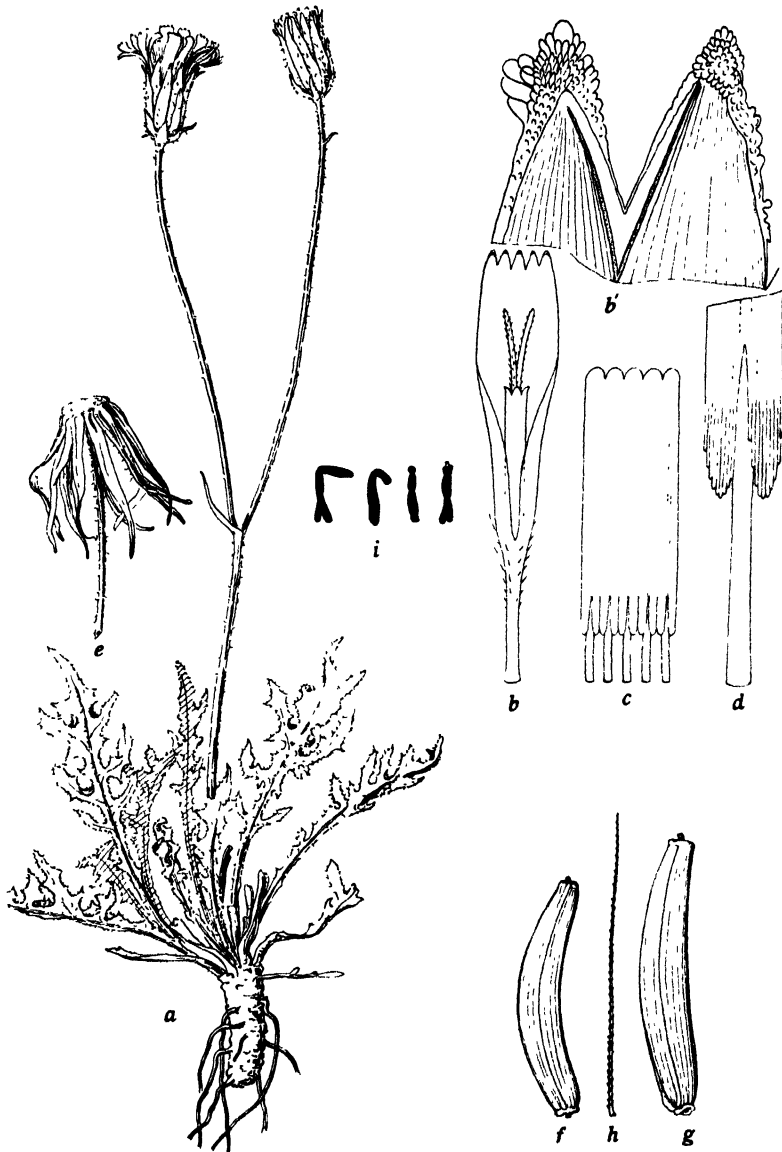


Fig. 30. *Crepis albiflora*, from Balls 1795 (UC 526631, hort. genet. Calif. 3312): *a*, plant, $\times 1$; *b*, floret lacking ovary, $\times 4$; *b'*, detail of ligule teeth, $\times 50$; *c*, anther tube, $\times 8$; *d*, detail of appendages, $\times 32$; *e*, old head, $\times 4$; *f-h*, 2 achenes and a pappus seta, $\times 8$; *i*, somatic chromosomes, $n = 4$, $\times 1250$. Type.

panulate, 10–11 mm long, 6–8 mm wide at middle, dark green, short and finely gland-pubescent; outer bracts 8, very unequal, longest $\frac{2}{3}$ as long as inner bracts, ovate to lanceolate, finely ciliate on margin; inner bracts 12–13, lanceolate, acute, or acuminate, ciliate at apex, ventrally glabrous, becoming dorsally carinate and spongy-thickened in fruit, ultimately reflexed; receptacle areolate, naked; corolla

about 14 mm long; ligule 2.5–3 mm wide, white; teeth 0.3–1 mm long, reddish-purple; corolla tube 4–4.5 mm long, pubescent, with 1–5-celled acicular hairs up to 0.5 mm long; anther tube yellow, 4.3×1.5 mm dis.; appendages 0.6 mm long, oblong, acute; filaments 0.75 mm longer; style branches 2.5 mm long, 0.15 mm wide, attenuate, yellow; achenes pale tawny, 3.75–4.5 mm long, 0.75 mm wide, \pm curved, subterete, about equally attenuate to both ends or less so upward, with slightly expanded pappus disk and lightly calloused base, about 20-ribbed, ribs narrow, rounded, smooth or muriculate; pappus white, 5 mm long, 2-seriate, the setae nearly equal in length and width, rather fine, soft, persistent. Flowering July–Aug.; flowers white, ligule teeth purple, anther tube, pollen, and style branches yellow. Chromosomes, $2n = 8$.

Known only from the type locality.

Monomorphic.

Turkey ("W. Armenia"): Kop Dag, Baiburt, 2440 m, open tops of hills, limestone scree, *Balls 1795* (UC 526631); ex hort. genet. Calif. 35.3312–2, cult. from seeds from type coll. (UC).

The plant was described by the collector as "3–5 inches tall, rosette flat on ground, leaves soft hairy, heads 1–1.25 inches in diameter, flowers blue-white with faint suggestion of mauve." It has been noted by the author that plants of this species, when grown in the garden, have the rosette flat on the ground in dry warm weather, but when grown in the greenhouse with uniform moisture the leaves are semierect. Freshly opened flowers in the greenhouse are nearly pure white; it may be that the suggestion of a blue or mauve tint develops with age of the flower head, especially under natural conditions. The few plants that I have been able to obtain from the original seed have been very difficult to bring to the flowering stage, although they lived for 2 or 3 years in pots in the greenhouse. Various exposures were tried, both in the greenhouse and outside.

Relationship

Crepis albiflora is closest to *C. dioritica* of Cilicia. The 2 species are similar in rhizome and leaf shape, but they differ greatly in the nature of the indumentum of leaves and stems, and in *C. dioritica* the involucre bracts are membranous-margined and the florets are smaller, with narrower anther tube and appendages. *C. albiflora* is less close to *C. heterotricha*, *C. pinnatifida*, and *C. bithynica*. In all 3 the rootstock is long and woody and the involucre, flowers, and achenes are different. Also, *C. bithynica* has 10 chromosomes in its somatic cells.

15. *Crepis dioritica* Schott. et Kotschy

Ex Boiss., Fl. Orient. 3: 842. 1875. (Fig. 31.)

Perennial, 0.5–0.9 dm high; rhizome short, vertical, praemorse, strongly fibrous; caudex 3–5 mm wide, brown, leafy at crown; leaves all caudical, 2.5–3.5 cm long, about 1 cm wide, oblanceolate, acute, pinnately parted, with oblong acute dentate segments, long- or short-petiolate, the petiole scarious, alate, densely pubescent, with short glandular and longer glandless white setiform hairs; stems 1 or 2, scapiform, 1–2-headed, 1–2-bracteate, slender, finely pubescent; heads erect, medium, 15–20-flowered, about 2 cm wide in anthesis; involucre campanulate, 9–10 mm high, 5–6 mm wide at middle, shortly and finely gland-pubescent; outer bracts 6–10, unequal, the longest $\frac{1}{2}$ as long as inner bracts, lanceolate, acute; inner bracts 10–15, lanceolate, acute, with pale scarious margins, glabrous on inner face (condition in fruiting heads not seen); corolla 12 mm long; ligule 1.5 mm wide, pubescent at base, with acicular hairs up to 0.4 mm long; teeth 0.3–0.6 mm long, obtuse;

corolla tube 3–4 mm long, very shortly pubescent near summit; anther tube 4.5×1.3 mm dis.; appendages 0.75 mm long, lanceolate, acute; filaments 0.5 mm longer; style branches 1–1.5 mm long, 0.1 mm wide, yellow; achenes (immature) dark brown, 5 mm long, fusiform, slightly constricted below the pappus disk, finely striate; pappus white or yellowish, 5 mm long, 2-seriate, the setae unequal, $20\text{--}50\mu$ wide at base, soft, tenacious. Flowering July; "ligules pale yellow."

Hieraciodes dioriticum O. Kuntze, Gen. 1: 345. 1891.

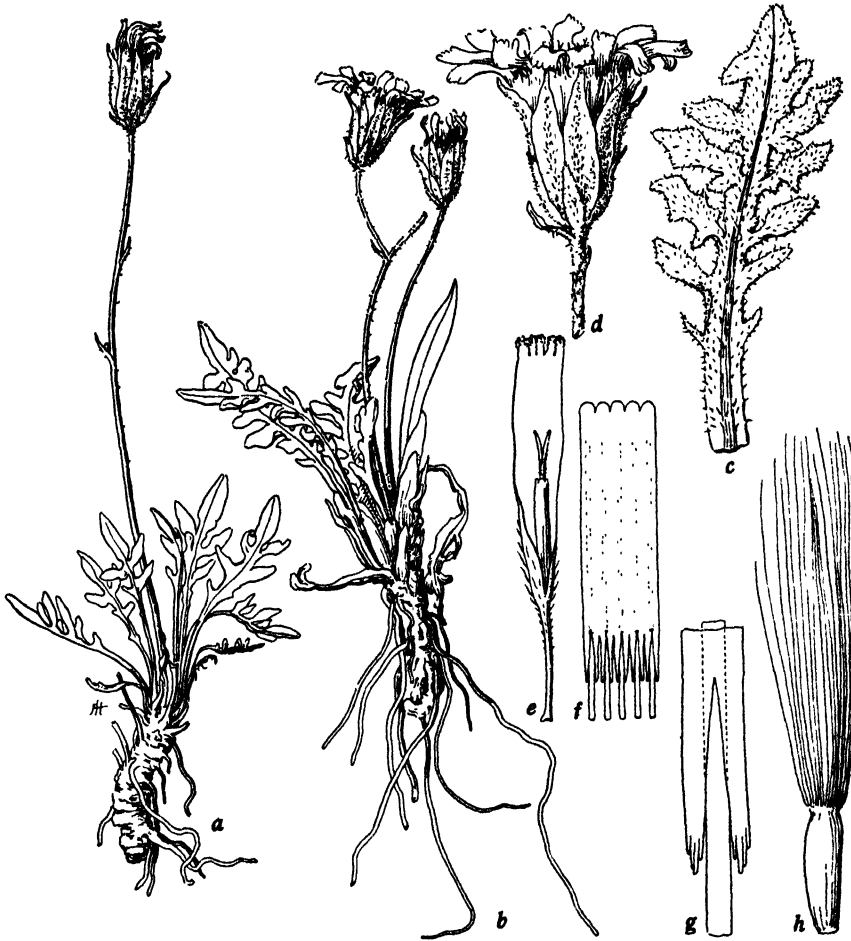


Fig. 31. *Crepis dioritica*, from Balansa in 1855 (US 132831, Bo): a, b, plants, $\times 1$; c, leaf, $\times 2$; d, head, $\times 2$; e, floret lacking ovary, $\times 4$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, young achene with pappus, $\times 8$.

Asia Minor, in S. Turkey, mountains of Cilicia, alpine (?). The altitude given in Fl. Orient. is 8000', whereas on the printed labels of the type collection the altitude given is 3000 ped. But the collection of Balansa in 1855 in Herb. Boissier has a label which reads: "Region alp. du Taurus oriental ..."

Monomorphic.

Turkey: Cilicia, Taurus, "Bulgar Dag," dioritic plains, near springs, Mt. Gisy Deppe, Kotschy 123 (type Bo, PC, Ms, Mu); E. Taurus, alpine reg., above Boulgarmaden (Bulghar Maden), Balansa 1028 in 1855 (Bo, US); without locality, Siehe in 1895–1896 (Genoa).

Relationship

Crepis dioritica is closest to *C. albiflora* of W. Armenia, from which it is very distinct in flower color, smaller florets, shorter style branches, longer and narrower anther appendages, and in the dark brown achenes, which are probably longer when mature. Although compared with *C. pinnatifida* by Boissier, it is less close to that species or to *C. heterotricha*. In both of these species the root is elongated and woody. Mature involucre and achenes of *C. dioritica* have not been seen.

SECTION 5. MESOMERIS

Relationships of the Species

The 8 species comprising this section fall naturally into 2 groups: (1) *C. lapsanoides*, *C. smyrnaea*, *C. lyrata*, and *C. mollis*; (2) *C. willemetioides*, *C. hierosolymitana*, *C. montana*, and *C. Mungierii*. The first 4 species exhibit strong resemblance to *C. viscidula* of sec. 1 in rhizome, stem, leaves, involucre, flowers, and fruits (including the persistent pappus in all but *C. mollis*); and they have no brown wool at the base of the caudical leaves. The second 4 species are definitely connected

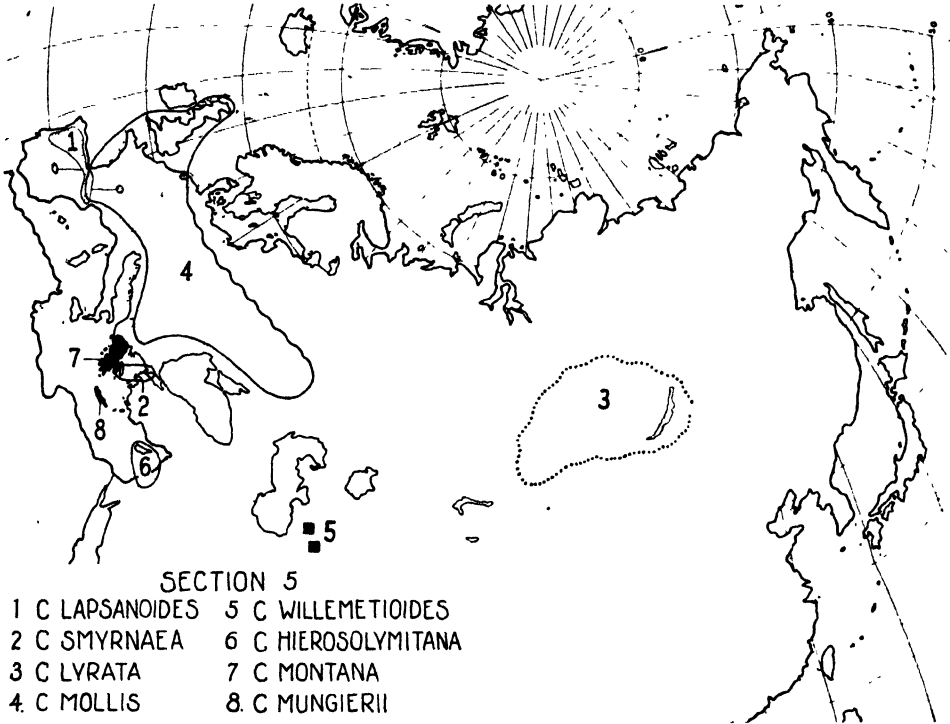


Fig. 32. Geographic distribution of the 8 species in sec. 5. The most primitive member of the section, *C. lapsanoides*, is restricted to the Iberian Pen. and is farthest from Central Asia, which, incidentally, is the western extremity of the range of *C. lyrata*. *C. mollis* is widespread in middle Europe. The other 5 species are restricted endemics, 4 of which are in the E. Mediterranean and 1 on the Iran-Turkestan border. Based on Goode *Base Map No. 201 PC*. By permission of the University of Chicago Press.

with the first group by the similarities between *C. willemetioides* and *C. lapsanoides* in rhizome, stem, leaves, involucre, and receptacle. But the other 3 species of the second group show greater reduction in size of the plant and most parts, together with the caducous pappus; and they all usually have brown wool at the base of the caudical leaves, although this may not be evident in fully mature plants.

All these species except *C. smyrnaea* have been examined cytologically and have been found to have 6 pairs of chromosomes. Although they exhibit some striking differences, especially in the satellite-bearing chromosomes, yet there is one point of similarity among all 7 karyotypes, viz., that there is always at least one large and one small pair with a median centromere. In this respect there is also general resemblance between these karyotypes and that of *C. pygmaea*. The last-named

species, aside from its tufted habit, also bears many resemblances to the species of this section and sec. 1. Therefore, Sec. Mesomeris is truly an intermediate group in that it is connected with some of the most primitive species in the genus and, at the same time, presents a considerable degree of reduction in size of the plant, leaves, heads, flowers, and fruits in both subgroups of the section.

The geographic distribution of this section agrees fairly well with Matthew's principle that the more primitive species are found farthest from the center of origin (see fig. 32). *C. lapsanoides* occurs only in the Iberian Pen., whereas the second group of 4 species are all close to Asia Minor, which may be assumed to be nearer to the region of origin of the genus. *C. lyrata*, of the Altai reg., and *C. mollis*, of W. and middle Europe, are intermediate with respect to area of distribution. *C. smyrnaca*, on the other hand, is from the Aegean reg. Although it shows the most similarity to *C. lapsanoides* of any species in the section, yet it is considerably more reduced than that species. Apparently, it is strictly local in distribution, and it may be a relic doomed to early extinction.

Key to the Species of Section 5

Corolla 17–18 mm long. Iberian Pen. or S. Siberia.

Involucre 10–11 mm long, 6–9 mm wide; outer bracts 8–12, $\frac{1}{4}$ – $\frac{1}{2}$ as long as the inner; bracts lance-linear, acuminate; achenes 5–6 mm long; pappus 5–6 mm long. Iberian Pen. 16. *C. lapsanoides*, p. 273

Involucre 7–9 mm long, 5–6 mm wide; outer bracts 8, about $\frac{1}{3}$ as long as the inner; inner bracts lanceolate, acute; achenes 3.5–4 mm long; pappus 4–5 mm long. S. Siberia 18. *C. lyrata*, p. 278

Corolla 9–13 mm long. Not in the Iberian Pen. or S. Siberia.

Leaves entire or denticulate; achenes 0.4–0.5 mm wide, 20-ribbed, reddish-brown. 19. *C. mollis*, p. 280

Leaves lyrate-pinnatifid; achenes 0.4–0.8 (mostly 0.5–0.7) mm wide, 10–15-ribbed or, if 20-ribbed (as sometimes in *C. montana*), then dark brown.

Plant 1-stemmed; stem cymosely branched above or the branches remote, paniculate; lower and middle cauline leaves large.

Corolla 13 mm long; receptacle ciliate. N. Persia. 20. *C. willemetoides*, p. 284

Corolla 9–10 mm long; receptacle glabrous.

Involucre gland-pubescent, the outer bracts $\frac{1}{4}$ – $\frac{1}{3}$ as long as the inner; corolla tube 3–4 mm long, pubescent only near base of ligule. 17. *C. smyrnaca*, p. 276

Involucre not gland pubescent, the outer bracts $\frac{1}{2}$ – $\frac{2}{3}$ as long as the inner; corolla tube 2–3 mm long, densely pubescent on upper half and on lower half of ligule 21. *C. hierosolymitana*, p. 286

Plant 1–4 stemmed; stems remotely 1–5 furcate; lower and middle cauline leaves small.

Heads about 25-flowered; ligules yellow, without red on outer face, the teeth very unequal; achenes 4–5 mm long, the ribs wider, smooth. 22. *C. montana*, p. 288

Heads 35–50-flowered; ligules yellow, with red on outer face, the teeth nearly equal; achenes 3–3.75 mm long, the ribs narrower, finely spiculate 23. *C. Mungierii*, p. 290

16. *Crepis lapsanoides* [*lampsanoides*] (Gouan) Tausch

Flora, 11 (Erg.): 79. 1828. (Fig. 33.)

Perennial, 3–9 dm high; rhizome horizontal, slender, bearing many long fibers, annually caulescent; caudical leaves borne at base of stem usually disappearing, sometimes persisting as a rosette, up to 12 cm long, 3 cm wide, oblanceolate, lyrate,

terminal segment nearly $\frac{1}{2}$ as long as the whole leaf, ovate, acute, denticulate to coarsely dentate, truncate to cordate, lateral segments small, in 2-4 opposite pairs, oblong-obtuse to triangular-acute, reduced toward the base, rachis and petiole narrowly winged, the whole leaf \pm pubescent with fine yellow glandless hairs; lower cauline leaves similar, except the petiole broader at the auriculate base, middle cauline leaves shorter, sublyrate or panduriform, with broad amplexicaul base, upper leaves gradually reduced, ovate to lanceolate, acuminate, sessile, amplexicaul; stem erect, terete, somewhat pithy or fistulose above, striate, pubescent like the leaves or glabrous, 2-6-branched at summit, branches short or the lower elongated, 1-2-headed; inflorescence cymose-corymbiform; peduncles 2-8 cm long, slightly thickened near head, pubescent with short fine pale or black hairs bearing brown or black glands; heads erect, medium to large, many-flowered; involucre dark green, cylindric to cup-shaped, 10-11 mm long, 6-9 mm wide at middle, gland-pubescent; outer bracts 8-12, unequal, longest $\frac{1}{3}$ - $\frac{1}{2}$ as long as inner bracts, lance-linear, acuminate; inner bracts 10-20, somewhat unequal, lanceolate, long acuminate, white-ciliate near apex, glabrous and strongly nerved on inner face, sometimes with a brown dorsal median nerve, becoming narrowly carinate and somewhat thickened dorsally at base in fruit; receptacle areolate, white-ciliate on interspaces; corolla 18 mm long; ligule 2.5 mm wide; teeth 0.5 mm long; corolla tube 4.5 mm long, pubescent with several-celled acicular hairs up to 0.4 mm long; anther tube 4×1.5 mm dis.; appendages 0.8 mm long, oblong, acute; filaments 2 mm longer; style branches 2 mm long, green; achenes brown, 5-6 mm long, 0.5-0.8 mm wide, columnar, slightly attenuate to both ends, constricted below the slightly expanded pappus disk and at the finely calloused hollow base, subterete, about 20-ribbed, ribs fine, rounded, smooth; pappus white or dusky white, 5-6 mm long, 2-seriate, the setae unequal in length and width, soft, persistent, exceeding the involucre. Flowering May-Aug.; flowers yellow. Chromosomes, $2n = 12$.

Hieracium lampsanoides Gouan, Ill. et Obs. Bot. 57, t. 21, f. 3, 1773.

Hieracium lapsanoides Willd., Sp. Pl., 3: 1580. 1800.

Crepis lapsanoides Tausch, Flora, 11 (Erg.): 79. 1828.

Geranium lampsanoides Rechb., ex Moessl., Handb. ed. 2, 1367 (in obs.). 1827-1829.

Soyeria lampsanoides Monn., Essai, 77. 1829.

Hieraciodes lampsanodes O. Kuntze, Gen. 1: 346. 1891.

Mountains of N. Portugal and N. Spain (with an outlying small area in central Spain [see below]), the Pyrenees, and W. France in the Corbières Mts., and an outlying station in Cantal; moist places in meadows, forests, and ravines. Adventive in Switzerland.

In the Montes de Toledo of central Spain, acc. to Willkomm (164), on forest meadows, *C. lapsanoides* occurs together with 3 other species of the Pyrenees, namely, *Ligusticum pyrenaicum*, *Geranium pyrenaicum*, and *Laserpitium latifolium*. This area, he states, is the southernmost extension of *Betula verrucosa* in W. Europe, and of numerous N. and middle European species. At the same time, many Mediterranean and several endemic species occur here. Although specimens from this area have not been seen by me, Willkomm (136) also reports this species from the Cantabrian-Asturican Mts., whence specimens are cited below. From the restricted and disjunct nature of its distribution, this must be considered a relic species, like *C. geracioides*.

The collection of living roots which provided the chromosome count reported above was made by my friend, Dr. J. Dufrenoy, in Hautes Garonne, near the axis separating these mountains from the Hautes Pyrenees. This locality is situated roughly about 10 km northwest of Bagnères de Luchon, in a narrow ravine contain-

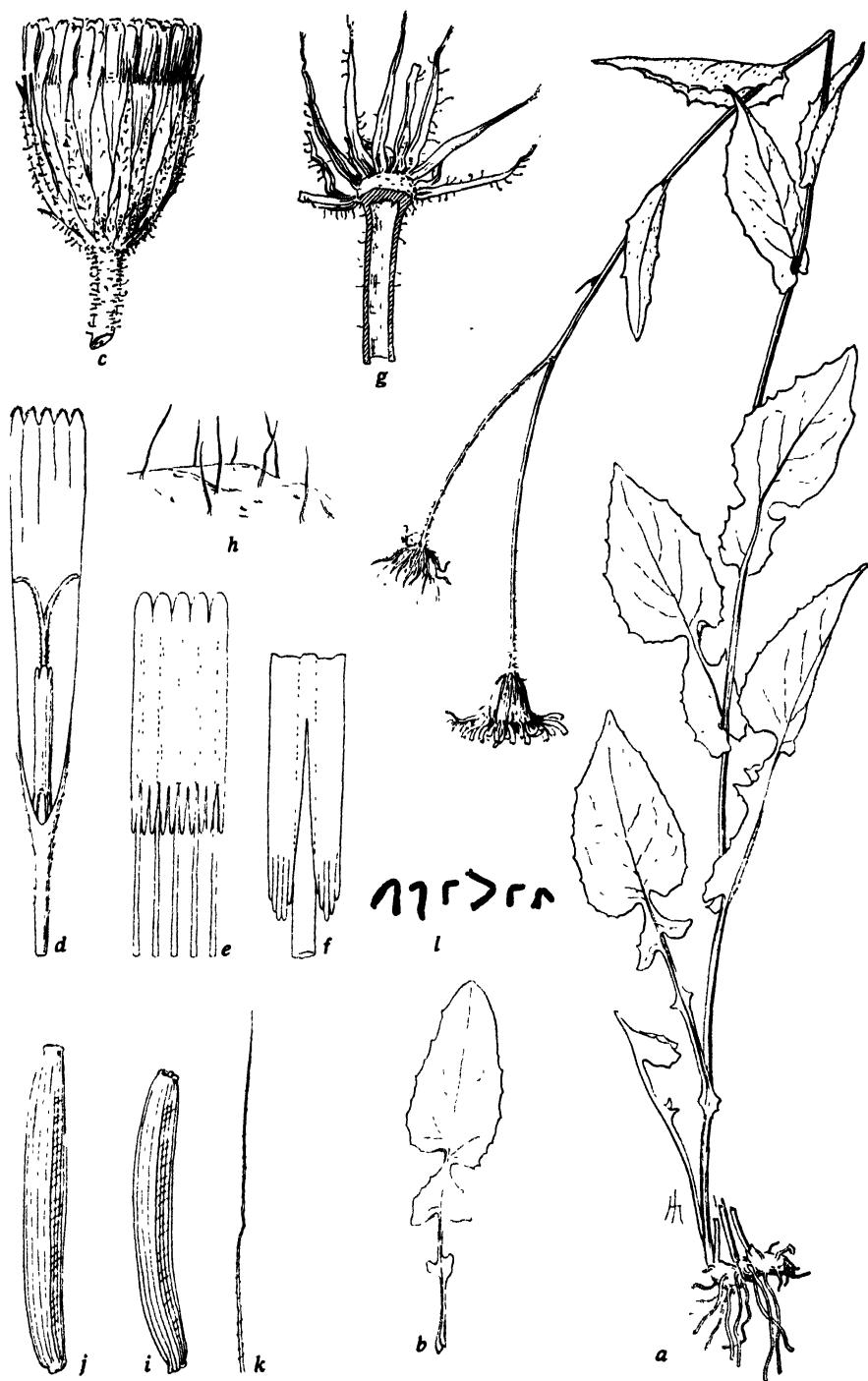


Fig. 33. *Crepis lapsanoides*, a, b, from Font Quer in 1912 (Bar); c-f, from Lomax in 1888 (UC 194338); g-k, from a specimen known to be typical; l, from hort. genet. Calif. 3466 (roots collected in Oredon Park, Hautes Pyrenees, France, by Dr. J. Dufrenoy): a, plant, $\times \frac{1}{2}$; b, caudical leaf, $\times \frac{1}{2}$; c, head, $\times 2$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, longitudinal section of a nearly mature head, $\times 2$; h, detail of receptacle, $\times 25$; i-k, 2 achenes and a pappus seta, $\times 8$; l, somatic chromosomes, $n = 6$, $\times 1250$.

ing a stream flowing into the Val de Luchon. Here, under a beech tree, was found one stand of about 25 plants. These were the only specimens of this species which could be found in that vicinity. Whether the plants of this species usually occur in such limited numbers at the other stations where it has been collected is not known to the present author. But from the very limited collections in the various herbaria where it is represented this appears probable. Its ecological relations resemble those of *C. geracioides*, which is also found in association with *Fagus silvatica* L.

The type of *Hieracium lapsanoides* Gouan has not been seen by me, but the specimens cited below agree with the best published descriptions.

The species is monomorphic, with minor variations in size, leaf shape, etc.

France: Cantal, Puy Mary, Claux, 1450 m, *Puyfol* in 1886 (Bur); Hautes Garonne, Luchon, Vol d'Oo, *Lomax* in 1888 (UC); *ibid.*, forêt de Montauban, 1200 m, *Luiset* in 1900 (Ms); *ibid.*, Luchon reg., *Pellat* in 1899 (Grenoble); Hautes Pyrénées, Gèdre, 1200 m, *Bodère* (Bur); *ibid.*, Gavarnie, Bois de Sarré, 1300 m, *Bodère* in 1885 (Bur). **Spain:** Catalonia, Pyrenees, La Rebuira, Prados, 1800 m, *Font Quer* in 1912 (Bar); Asturias, Puerto de Leitariegos, *Durieu* in 1835 (DC Prod. vii: 169 n. 47, photograph UC); *ibid.*, between Cangas and Leitariegos, in 1868 (RB, photograph UC). **Portugal:** Serra da Estrella, Covao de Metade, *Daveau* in 1881 (Ms); Minho, Gerez, in 1877 (K); Traz-os-Montes, Serra de Nogueira, 1150 m, *Gandoger* in 1905 (Mo).

Relationship

Crepis lapsanoides resembles *C. viscidula* of sec. 1 in habit, leaf shape, type of involucre, flowers, and fruits. These resemblances indicate a close connection between the 2 sections. Next to *C. lapsanoides* stands *C. symrnaea*, which has not been examined cytologically, but which probably has 6 pairs of chromosomes. *C. lapsanoides* differs from *C. symrnaea* in the usually taller stature of the plant, much larger heads, ciliate receptacle, very much larger florets, and longer achenes and pappus. The color of the pappus in both species is somewhat variable. The 2 species occupy widely separated areas.

17. *Crepis symrnaea* DC.

Prod. 7: 170. 1838. (Fig. 34.)

Perennial, 2–6 dm high; rhizome vertical, praemorse, bearing fleshy fibers; caudex simple or 1-furcate, leafy, 1-stemmed; caudical leaves few, mostly persisting, pubescent with fine yellow glandless hairs, up to 25 cm long, 6 cm wide, oblanceolate, lyrate, the terminal segment $\frac{1}{4}$ – $\frac{1}{3}$ as long as the whole leaf, ovate, acute or acuminate, dentate, the base cordate or truncate, lateral segments smaller, in 1 or 2 opposite pairs, oblong-obtuse to triangular-acute, rachis and petiole narrowly winged; lower cauline leaves similar or panduriform, middle and upper cauline leaves lanceolate to ovate, sessile, amplexicaul, acute or acuminate, denticulate, uppermost bractlike; stem erect, terete, striate, finely pubescent, glandular toward summit, 2–8-branched above, branches elongated, 1–10-headed, inflorescence paniculate-corymbiform; peduncles 2–5 cm long, slightly thickened near head, shortly and finely gland-pubescent, the glands very dark; heads erect, medium to small, 30–40-flowered; involucre yellowish or brownish-green, cylindric-campulate, 10–11 mm long, 6–7 mm wide at middle in fruit, gland-pubescent; outer bracts 10–12, unequal, longest $\frac{1}{4}$ – $\frac{1}{3}$ as long as the inner, lance-linear, acuminate; inner bracts 13–18, in 2 sometimes unequal series, lanceolate, acuminate, glabrous and strongly nerved on inner face, becoming weakly carinate dorsally and spongy-thickened at base in fruit; receptacle areolate-fimbriate, fimbriae low, fleshy, naked; corolla 9–10 mm long; ligule 1.25 mm wide; teeth 0.2 mm long, very glandular; corolla tube 3.5 mm long, pubescent at summit with acicular hairs up to 1 mm

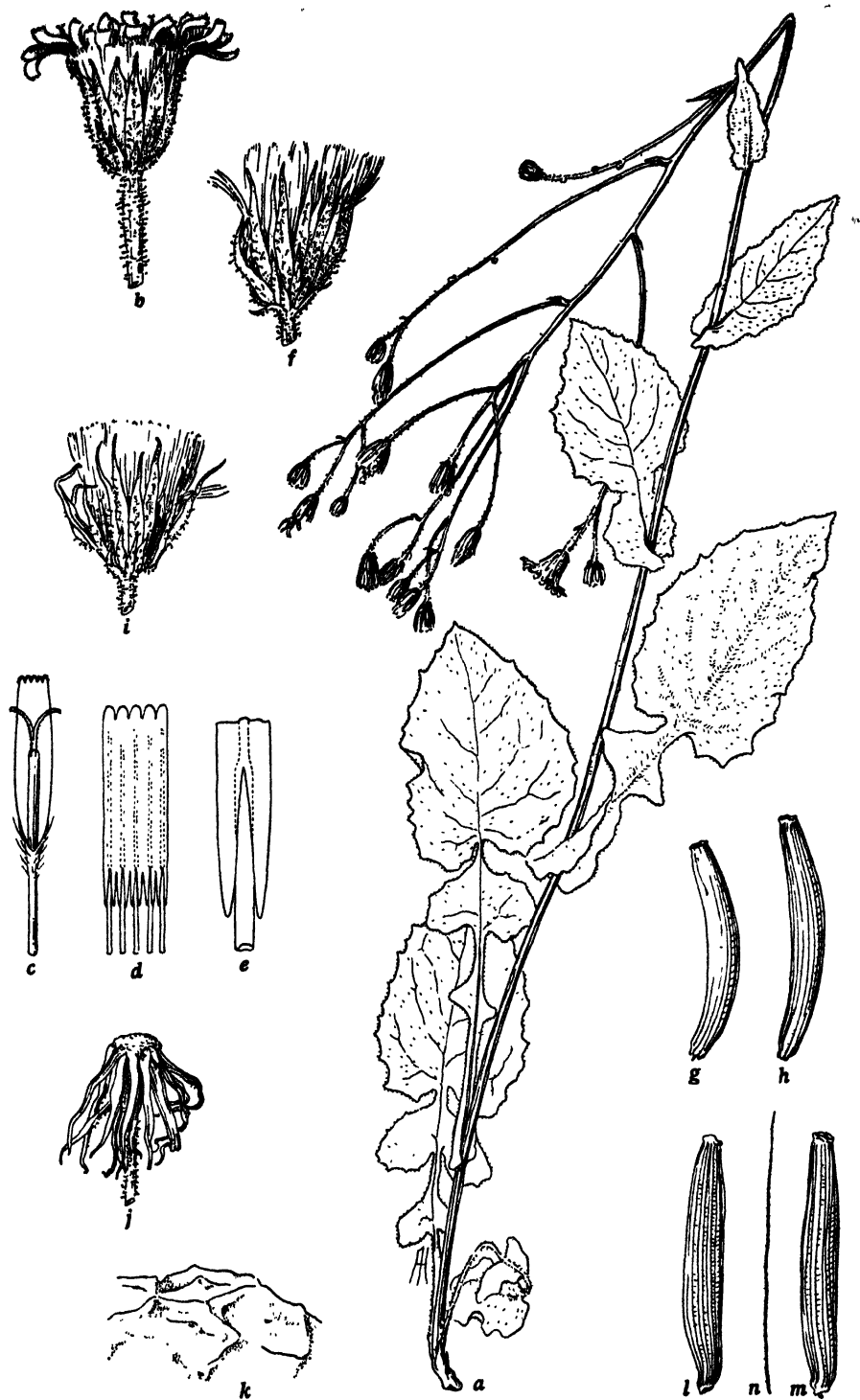


Fig. 34. *Crepis smyrnaea*, a-e, from Bornmüller 5236 (PA); f, from Asnavour in 1898 (Bur); g, h, from Murmann, type of *C. Murmanni* (Bo); i-n, from Haussknecht in 1885 (B): a, plant, $\times \frac{1}{2}$; b, head, $\times 2$; c, floret lacking ovary, $\times 4$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, head, $\times 2$; g, h, 2 achenes, $\times 8$; i, j, heads, $\times 2$; k, detail of receptacle, $\times 25$; l-n, 2 achenes and a pappus seta, $\times 8$.

long; anther tube 3.5×1.2 mm dis.; appendages 0.6 mm long, lanceolate, acuminate; filaments 0.75 mm longer; style branches about 1 mm long, green; achenes brown, 3.8–4.5 mm long, 0.5–0.6 mm wide, fusiform, constricted below the scarcely expanded white pappus disk and above the finely calloused hollow base, subterete, 10–15-ribbed, ribs narrow, rounded, smooth; pappus pale tawny, 5 mm long, 1–2-seriate, nearly equal, rather fine, soft, persistent, not exceeding the involucre. Flowering May–July; flowers yellow.

C. Murmanni Boiss., Fl. Orient. Suppl. 325. 1888.

Hieraciodes smyrnaeum O. Kuntze, Gen. 1: 346. 1891.

This little-known polymorphic species consists apparently of 3 distinct local races: one on Mt. Olympus, near Brussa, Bithynia; another in the vicinity of Constantinople; and a third on Mt. Pentelikon, in Attica, Greece. No other specimens except the type are known from the type locality, Smyrna; but a fourth race may exist near that place. Future collections may establish a more extensive distribution.

Turkey: Smyrna, *Aucher-Eloy* in 1837 (DC) type; Bithynia, Olympus, near Brussa, among *Juniper* bushes, *Pichler* in 1873 (Bo, G); *ibid.*, alpine (?) region, among *Juniper*, *Pichler* in 1874 (Bo, RB, Fl, UCf); Olympus, *Pichler* in (?) 1870 (US); Bithynia, Mt. Olympus (Keschischdag, among shrubs, 200 m, *Bornmüller 5236* (UWG, PA); Constantinople, near Flemur, hills, limy soil, *Murmann* (Bo, UCf, RB) m.v. 1; Constantinople, woods near Bujukdere, *Murmann* (Bur, received in 1876) m.v. 1; Constantinople, woods near Guenksouyou, *Asnavour* in 1898 (Bur) m.v. 1. **Greece:** Attica, Mt. Pentelikon, among shrubs, *Haussknecht* in 1885 (B, UCf) m.v. 2.

Minor Variants of *Crepis smyrnaca*

1. (*C. Murmanni* Boiss., Fl. Orient. Suppl. 325. 1888.) The branches are arranged in the form of an umbel, at least in the type of this form; and the pappus is lighter in color than in the type of the species. *Murmann* (type of *C. Murmanni* Bo, RB), hills near Flemur, Constantinople; *Murmann* (Bur, received in 1876), woods near Bujukdere, Constantinople; *Asnavour* in 1898 (Bur), woods near "barrage" of Guenksouyou, Constantinople, Turkey.

2. The caudical leaves resemble those of *C. Reuteriana*. *Haussknecht* in 1885 (B), among shrubs, Mt. Pentelikon, Attica, Greece.

Relationship

Crepis smyrnaca is closest to *C. lapsanoides*, from which it is easily distinguished by the much smaller flower heads, the glabrous receptacle, very much smaller florets, shorter achenes and pappus, and, at least in typical forms, the tawny pappus. It is less close to *C. montana* and *C. Reuteriana*, with which it has been compared in earlier descriptions.

18. *Crepis lyrata* (L.) Froel.

Ex DC., Prod. 7: 170. 1838. (Fig. 35.)

Perennial, 3–6.5 dm high; caudex short; rhizome slender, praemorse, fibrillate; caudical leaves 12–24 cm long, 3–5 cm wide, obovate-oblong, denticulate to coarsely dentate, repand, sinuous, or lyrate-pinnatifid, gradually reduced into a long winged petiole, sparsely pubescent with short yellow hairs; lower cauline leaves similar or with a broader petiole approaching panduriform, auriculate-amplexicaul, the others oblong or lanceolate, acute, sessile, auriculate-amplexicaul, uppermost bract-like; stem erect, terete, sulcate, fistulose, sparsely pubescent with yellow glandless hairs, shortly branched near the top, forming a small few-headed corymbiform cyme, or paniculately branched from middle or near base, the branches strict, few-headed; peduncles 1–3(5) cm long, slender, slightly thickened near the head, densely gland-pubescent; heads erect, small, 35–45-flowered; involucre campanulate, 7–9 mm long, 5–6 mm wide at middle in fruit, dark green, densely gland-pubescent;

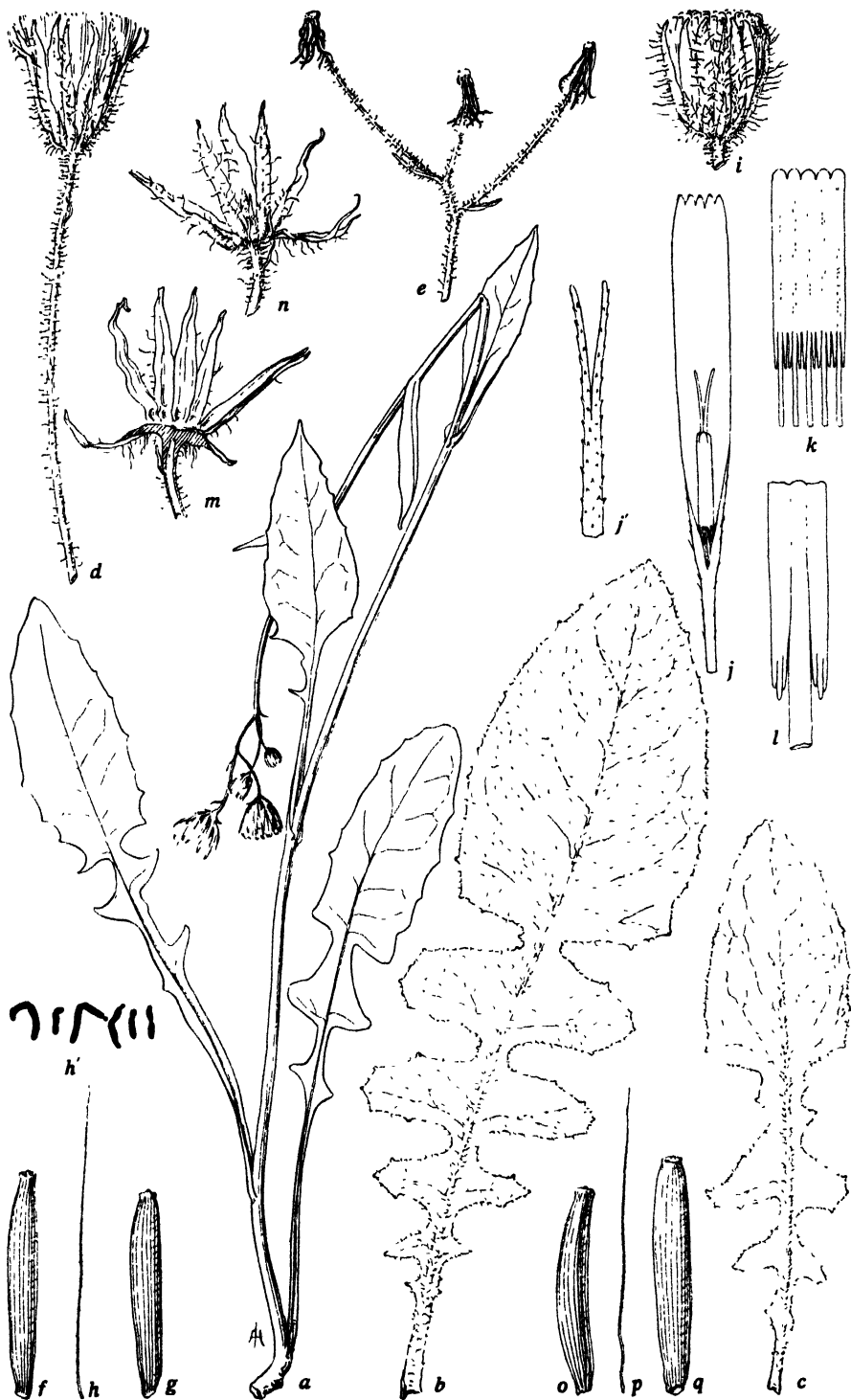


Fig. 35. *Crepis lyrata*, a, from type (L); b-h', from hort. genet. Calif. 1644 (UC 531724); i-q, from Turczaninow in 1835 or 1840 (Bo): a, plant, $\times \frac{1}{2}$; b, c, caudical leaves, $\times 1$; d, head and peduncle, $\times 2$; e, part of inflorescence, $\times 1$; f-h, 2 achenes and a pappus seta, $\times 8$; h', somatic chromosomes, $n = 6$, $\times 1250$; i, young head, $\times 2$; j, j', floret lacking ovary, $\times 4$; k, anther tube, $\times 8$; l, detail of appendages, $\times 32$; m, n, mature involucre, longitudinal section, inner and outer face, $\times 2$; o-q, 2 achenes and a pappus seta, $\times 8$.

outer bracts about 8, unequal, longest $\frac{1}{3}$ as long as inner bracts, subulate, acute; inner bracts 12–14, lanceolate, acute, glabrous on inner face, dorsally carinate and spongy-thickened near base in fruit; receptacle areolate, naked; corolla about 17 mm long; ligule 2 mm wide; teeth 0.3–0.5 mm long; corolla tube 3–5 mm long, pubescent with several-celled acicular hairs up to 0.5 mm long; anther tube 3.5×1.25 mm dis.; style branches about 2 mm long, 0.1 mm wide, light or dark yellowish-green; achenes brown, 3.5–4 mm long, 0.5–0.6 mm wide, fusiform, slightly constricted below the pale narrow pappus disk, strongly constricted at the finely calloused hollow base, 20-striate, striae narrow, close, rounded, smooth; pappus white, 4–5 mm long, 1–2-seriate, fine, soft, persistent, slightly exceeding the involucre. Flowering June–July, *fide* Turczaninow; flowers yellow. Chromosomes, $2n = 12$.

Hieracium lyratum L., Sp. Pl. 2: 803. 1753.

Crepis hieracioides Ledeb., Fl. Alt. 4: 126. 1833 non W. K.

Aracium lyratum Herd., Bull. Soc. Nat. Mosc. 43: 214. 1870.

Hieraciodes lyratum O. Kuntze, Gen. 1: 346. 1891.

S. Siberia, in the Altai, Tomsk, Jenisseisk, Irkutsk, and Baikal regions; river valleys, forest clearings, along banks of streams, and in moist meadows; lower montane to subalpine elevations.

Monomorphic.

Siberia: Without locality (L), type of *H. lyratum*; Altai, *Ledebour* (K, B); Altai, *Duhmberg* 286 (B, UCf); Altai, *Ludwig* (US); Tomsk Prov., near Tomsk, *Krylow* in 1902 (B, VG); Jenisseisk Prov., Minussinsk dist., growing in moss, *Kusnezow* in 1913 (NY); Jenisseisk Prov., Krassnojarsk, *Turczaninow* in 1840 (Bo, UCf, K), as *C. hieracioides*; Baikal reg., Chara Murin, *Turczaninow* in 1835 (K).

Relationship

Crepis lyrata is closest to *C. lapsanoides* and *C. smyrnaea*, from both of which it is distinct in the intermediate flower size, the shorter achenes, and the mostly 1-seriate pappus. Next stands the European species, *C. mollis*, which differs consistently in leaf shape, in the somewhat larger heads, the longer and narrower anther tube, the reddish-brown, slightly narrower achenes, and the more copious pappus. In view of the remarkable similarity between the flowers and fruits of *C. lyrata* and those of *C. mollis*, the striking differences in their karyotypes are particularly noteworthy.

19. *Crepis mollis* (Jacq.) Ascherson

Fl. Brand. 386. 1864. (Fig. 36.)

Perennial, 3–7.5(9) dm high; rhizome 0.5–3 cm long, praemorse, bearing long fleshy fibers; caudex very short, 3–5 mm wide, 1-stemmed, leafy; caudical leaves 4–27 cm long, 1.5–5 cm wide, elliptic to oblanceolate, obtuse or acute, entire or merely denticulate, gradually or abruptly attenuate into a long or short winged petiole, with entire margin, \pm pubescent with fine yellow glandless hairs or glabrous; lower cauline leaves similar or sessile, middle ones few, remote, mostly lanceolate, acute, sessile, amplexicaul, uppermost reduced, bractlike; stem erect, slender, 1–5 mm wide at base, terete, fistulose, \pm pubescent below like leaves or glabrous, branched from or above the middle, aggregate inflorescence corymbiform; branches approaching or equal to axis, 1–4-headed; peduncles 1–9 cm long, \pm pubescent with fine short or unequal gland hairs, tomentulose and somewhat thickened near head in fruit; heads erect, medium, many-flowered; involucre 8–10 (12) mm long, 5–6 mm wide at middle, dark green, \pm gland-pubescent, hairs short or

long or mixed, black with black glands or green with yellow or brown glands; outer bracts 8–10, unequal, longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as inner ones, lanceolate, acuminate, white-ciliate at the apex; inner bracts 12–18, in 2 ranks, inner ones narrower, lanceolate, acute or acuminate, white-ciliate at the apex, becoming carinate and spongy-thickened dorsally in fruit, ventrally glabrous; receptacle areolate, obscurely fimbriate, glabrous; corolla about 13 mm long; ligule 2 mm wide, pubescent near base; ligule teeth 0.15–0.25 mm long, purplish or yellowish; corolla tube about 3.5 mm long, pubescent with 1–3-celled acicular hairs 0.1–0.5 mm long; anther tube about 3.75×1 mm dis.; appendages 0.5 mm long, oblong, acute; filaments 1 mm longer; style branches 2 mm long, 0.1 mm wide, attenuate, dark green; achenes reddish-brown, 3–4.5 mm long, 0.5–0.7 mm wide, marginal curved, inner straight, gradually attenuate to apex and base, with slightly expanded pale pappus disk and yellowish callosities enclosing the hollow base, about 20-ribbed, ribs narrow, rounded, smooth, nearly equal but often with 2–4 definitely wider; pappus white, 5–6 mm long, 2-seriate, outer bristles shorter and finer, united at base, soft, deciduous. Flowering June–Aug.; flowers golden yellow. Chromosomes, $2n = 12$.

Hieracium molle Jacq., Fl. Aust. 2: 12, tab. 119. 1774.

H. succisaefolium All., Fl. Ped. 1: 215. 1789.

Crepis hieracioides W. et K., Pl. Bar. Hung. 1: 71. 1802 et Willd., Sp. Pl. 3: 1601. 1804.

H. croaticum W. et K., *op. cit.*, 3: 242 (267 ♀), t. 218. non Lap.

H. Sternbergii Hoppe, ex Horn., Suppl. Hort. Hafn. 90, 1819.

C. succisaefolia Tausch, Flora 11 (Erg.): 79. 1828.

C. croatica Froel., ex DC., Prod. 7: 170. 1838; Schloss. et Vukot., Fl. Croatica 883. 1869.

Hieraciodes molle O. Kuntze, Gen. 1: 345. 1891.

C. Velenovskyi Domin, Sitz. Böhm. Ges. Wiss. Jahr. 1904, n. 18: 37. 1905.

C. mollis subsp. *eumollis* Domin, subsp. *hieracioides* (W. et K.) Domin, et subsp. *Velenovskyi* (Dom.) Domin, Preslia (Vest. Českoslov. Bot. Spol. Praze) 13–15: 252. 1935.

The following critical specimens have been examined by the author and their close correspondence noted: *H. molle* Jacq., and *H. succisaefolium* All., in Herb. DC.; *C. hieracioides* Kit., in Herb. Willd. n. 14746–1; *H. croaticum* Kit., in Herb. Willd. n. 14690–1; *C. succisaefolia* var. *hirta* (Tausch no. 915b) in Herb. Prag.

Great Britain and from the Pyrenees eastward through the mountains of middle Europe, as far south as Serbia and S.W. Bulgaria, to middle and S. Russia; wooded or open often moist places on plains, hills, and mountain slopes, up to 370 m in N. England, to 1270 m in the Pyrenees, and to 2000 m in Bavaria and Bulgaria.

Classified (as *C. succissifolia*) by Pax (1: 227) as of the middle European element of the W. Carpathian Mts., this species occurs in treeless meadow bogs in the foothill reg. and at low elevations in the higher mountains. Drude (605) lists it as a "Characterart" of the meadow formation in the Bohemian and Bavarian forests.

Differences in amount of pubescence on leaves and stem, in the entire or denticulate leaf margins, in degree of robustness and number of cauline leaves and heads, in thickness and firmness of stem and leaves, in point of origin of the lowest branch, in depth of yellow color of the flowers, and in color of the involucre hairs have been used by various authors for recognition of named varieties and, in one instance (Domin, Sitz. Böhm. Ges. Wiss. Jahr. 1904, n. 18: 37–39), for subspecies (see m.v. 1). Many of these variations are probably due to environmental differences, but some of them, like presence and absence of pubescence or color of hairs and glands, may be caused by genic differences. Yet such inherited differences must be considered of minor importance unless they are associated with other genetic differences of a more fundamental nature. Accordingly, none of the named varieties and forms of this species (cf. de Candolle, 170; Fiori, 440; Rouy, 222; Hegi, 1156) is listed below as a numbered variant.

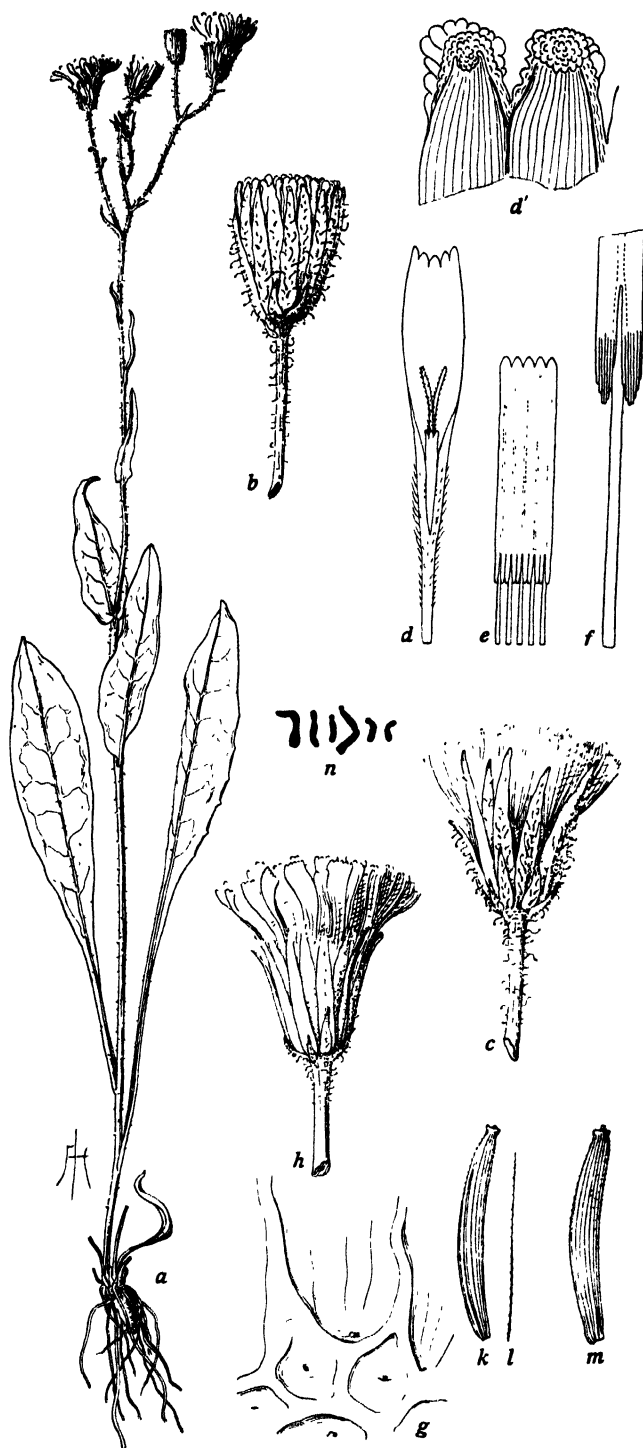


Fig. 36. *Crepis mollis*, a-g, from Laus in 1930 (UC 463912); h, from Felsman in 1885 (UC 452791); k, l, from Kitaibel (BW 14680-1); m, from Duhmberg 286 (B); n, from hort. genet. Calif. 2201 (seed received from Lwow Bot. Gard. through Dr. M. Navashin): a, plant, $\times \frac{1}{2}$; b, c, heads, $\times 2$; d, floret lacking ovary, $\times 4$; d', detail of ligule teeth, $\times 50$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, detail of receptacle and base of bract, $\times 25$; h, head, $\times 2$; k-m, achenes and pappus seta, $\times 8$; n, somatic chromosomes, $n = 6$, $\times 1250$.

It has been claimed by Domin and others that distinct geographic races or subspecies can be recognized on the basis of such variations as those noted above. But, as Hegi points out, the distribution of the several forms has not been studied sufficiently to permit this recognition. I find, however, that even a limited number of collections from a single region may contain most of these variations. This is true, for example, of the specimens shown on eleven sheets in the Herbarium of the Botanical Society and Exchange Club of the British Isles. These specimens represent sixteen collections from N. England and S. Scotland and include various combinations of the superficial differences noted above. Hence, it seems probable that this species, like many others in the genus, consists of a mixture of minor forms, partly genetic and partly ecologic in nature. At the same time, the idea of Domin (*loc. cit.*) and Beck (Fl. Nied. Oest. 2: 1275) that in central Europe the forms from higher altitudes are more robust and have firmer stems and leaves and blackish pubescence, whereas those from lower altitudes are more slender and have thinner leaves and paler pubescence, may have a factual basis. If so, then, the situation is similar to that in *C. capillaris*, in which the forms from northern regions are more robust and have larger heads, florets, and fruits, whereas those from more southern districts, especially S. Spain, are smaller and more pubescent. But only by more extensive collections and field studies can it be determined whether there are enough constant differences between the forms of the 2 regions to warrant the recognition of subspecies.

Great Britain: Scotland, Aberdeen, Corrymulzie Falls, *Druce* in 1878 (Oxford); Scotland, Perth, near Garth Castle, *Schoolbred* in 1913 (Oxford); England, Cumberland, Alston, *Waterfall* in 1921 (Oxford); England, N.W. Yorkshire, Lonton, Fairy Knoll, *Lees* in 1875 (Oxford). **Spain:** Pyrenees, La Cerdana, Estovar, and Llivia, *Sennen 6121, 6122* (US). **France:** Aude, St. Laurent, *Marty* (Bur); Aveyron, Bois d'Aubrac, *Soulie* in 1901 (Bur); Puy-de-Dome, Clermont-Ferrand, *d'Alleizette* in 1931 (UC); Ain, Recuber, *Fray* in 1882 (K); Jura, *Haller 47* (DC). **Switzerland:** near Neuchatel, *Tripet* in 1870, 1871, 1879 (Bur, DS). **Germany:** Königsberg, *Caspary* in 1859 (Ya); Bavaria, Augsburg, *G. G.* in 1868 (CA); Bavaria, Kempten, *Zick* in 1913 (Bur); Saxony, Geising, *Missbach* in 1908 (US); Thuringia, *Wallroth* in 1834 (DC); Harz, Ruthigesdort, *Focke* in 1878 (US). **Austria-Hungary:** Upper Austria, Aistersheim, *Keck* in 1875, 1882 (Bur, UC); Schneeberg, *Halácsy* in 1880 (UWH); Salzburg, Juvavia, near Aigen, *Stohl* (Bur, Minn); Choos Mts., above Lucsky, *Pantocsek* (Bur, Minn); Hungary, *Kitabel* (BW) as *Hieracium molle* Froel. **Yugoslavia:** Croatia, *Kitabel* (BW) as *H. molle* Froel. **Bulgaria:** Mt. Pirin, *Georgieff* in 1932 (UC). **Czechoslovakia:** Bohemia, Ebersdorf, *Wiesbaur* in 1885 (US); Moravia, Schmeil, *Lichtzibache, Lans* in 1907 (US). **Lithuania:** ex herb. Fischer (Bur). **Russia:** Volin Prov., Kremenetz, *Kopssinski* in 1893 (Lenin).

Minor Variant of Crepis mollis

1. (*C. Velenovskyi* Domin, Sitz. Böhm. Ges. Wiss. Jahr. 1904, n. 18: 37. 1905.) Described as a race of *C. succisaefolia* sen. lat., distinguished by its very large entire thin soft leaves, the elongated corymb, and small heads. Being an inhabitant of lowlands, it is rather probable that this plant is merely an extreme ecologic modification. Known from only one locality, at Sadska, in Elbetal, Bohemia, Czechoslovakia.

Relationship

Crepis mollis is closest to *C. lyrata*, from which it is distinguished by the entire or merely denticulate leaves, the larger involucre, and the narrower reddish-brown achenes. The geographic areas of the 2 species are also distinct, since *C. lyrata* is known only from Siberia. The wide distribution of *C. mollis*, as compared with *C. lyrata*, is evidently associated with a certain degree of reduction, notably in the achenes and flower parts. From this standpoint the entire leaves of *C. mollis* may be considered a reduced state of the lyrate leaves characteristic of this section. The resemblance in shape of its leaves to those of *C. kashmirica* is offset by its much closer resemblance in habit, involucre, flowers, and fruits to the other species of this section.

20. *Crepis willemetioides* Boiss.

Fl. Orient. 3: 845. 1875. (Fig. 37.)

Perennial, 2.5–7 dm high; rhizome horizontal, praemorse, 1–2 cm long, 0.5 cm wide, bearing strong fleshy fibers; caudex short, leafy, with brown wool at the base of the caudical leaves evident in younger plants but disappearing later; leaves glabrous or pubescent with pale setiform glandless hairs; caudical leaves few, ascending, 8–25 cm long, 1.5–6 cm wide, oblanceolate, lyrate-pinnatifid, terminal segment 3–8 cm long, ovate or elliptic, cordate, acute or obtuse, sinuate, dentate or denticulate, lateral segments 6–8, remote, mostly opposite, oblong-obtuse or irregularly angular, gradually reduced to the long narrow petiole; cauline leaves 4–6, sessile, oblanceolate, cordate-amplexicaul, acute, dentate or denticulate, the lower large, the others gradually reduced, uppermost bractlike; stems 1 or 2, erect, striate, glabrous or sparsely pubescent with fine glandless hairs below, branched above, branches remote, long, 1–2-headed, inflorescence cymose-corymbiform; peduncles 1.5–7.5 cm long, slender, not thickened at base of head, glabrous or pubescent with short fine gland hairs, glands brown or black; heads erect, medium, about 40-flowered; involucre cylindric-campanulate, 9–10 mm high, 5–6 mm wide at middle in fruiting heads, pubescent with short and/or long gland hairs, ultimately reflexed; outer bracts 10, unequal, longest $\frac{1}{2}$ as long as inner ones, lanceolate, acute; inner bracts 16–20, lanceolate, acute or acuminate, ciliate at the apex, dorsally keeled, becoming spongy-thickened near the base, ventrally glabrous; receptacle areolate-fimbriate, fimbriae low, ciliate, cilia up to 0.6 mm long; corolla 13 mm long; ligule 2 mm wide, teeth 0.3–0.4 mm long, obtuse; corolla tube 3 mm long, very slender, densely pubescent above with acicular hairs 0.4–0.8 mm long; anther tube 4×1 mm wide dis.; appendages 0.7–0.9 mm long, narrow, acuminate; filaments 0.5 mm longer; style branches 2.5 mm long, 0.15 mm wide, green; achenes dark brown, 4 mm long, fusiform, terete, moderately attenuate to the scarcely expanded white pappus disk, \pm curved, abruptly constricted near the very small hollow calloused base, about 15-ribbed, ribs narrow (up to 0.1 mm wide), smooth or finely rugulose under lens; pappus white, 5–7 mm long, 2-seriate, fine, soft, caducous. Flowering Apr.–June; flowers deep yellow, without red. Chromosomes, $2n = 12$.

Hieraciodes willemetioides O. Kuntze, Gen. 1: 346. 1891.

Monomorphic.

N.E. Persia: near Siaret, *Bunge 275* (Bo) type. **Transcasian Prov.:** Turcomania, near Persian frontier, Kopet-dagh Mts., Mt. Hosar-dagh, near the town of Karakala, rocky slope covered with dwarf trees, *Popov* in 1931 (UC); *ibid.*, ex hort. genet. Calif. 35.3217–8–9, cult. from seeds collected by Popov (UC).

Relationship

As noted by Boissier (*loc. cit.*), this little-known species is closely related to *C. hierosolymitana* and *C. montana*, although very distinct from both in the horizontal rhizome, the leaf shape, which resembles that of *C. lapsanoides*, the ciliate receptacle, the narrow acuminate anther appendages, and the longer pappus. *C. willemetioides* shows more resemblance to *C. lapsanoides* than do the 3 following species in the strong horizontal rootstock, tall stature, large similarly shaped leaves, and ciliate receptacle. The chromosome complement most nearly resembles that of *C. hierosolymitana*. The cultivated plants cited above faithfully reproduced the distinctive features of the species, although, because they were grown in pots, they were only half as large as the wild specimens.

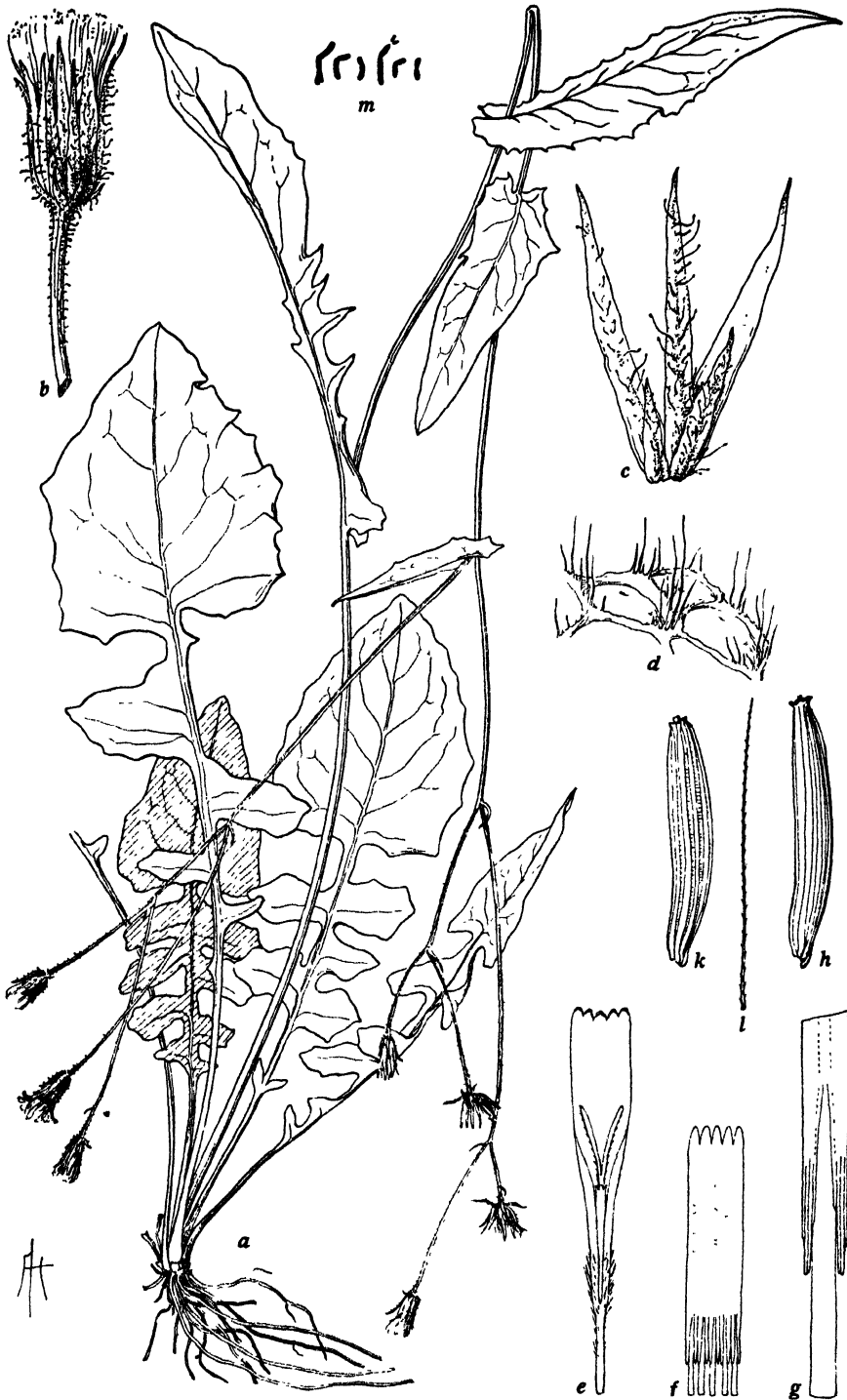


Fig. 37. *Crepis willmetioides*, from Popov in 1931 (UC 489442 = hort. genet. Calif. 3217): *a*, plant, $\times \frac{1}{4}$; *b*, head, $\times 2$; *c*, 3 inner involucre bracts united at base, outer face, $\times 4$; *d*, detail of receptacle, $\times 25$; *e*, floret lacking ovary, $\times 4$; *f*, anther tube, $\times 8$; *g*, detail of appendages, $\times 32$; *h*, *k*, *l*, 2 achenes and a pappus seta, $\times 8$; *m*, somatic chromosomes, $n = 6$, $\times 1250$.

21. *Crepis hierosolymitana* Boiss.

Diag. Pl. Orien. Nov. ser. 1, 11: 54. 1849. (Fig. 38.)

Perennial, 1.5–4 dm high; rhizome short, thick, praemorse, bearing numerous fleshy fibers; caudex 7–10 mm wide, naked or brown-wooly at base of petioles; basal leaves up to 12 cm long and 2.5 cm wide, oblanceolate, lyrate-pinnately parted, terminal segment oblong-ovate, obtuse, repand or sinuate-denticulate, base truncate or subcordate, lateral segments 8–10, diminishing toward petiole, oblong-ovate, obtuse, repand, tapering to the narrowly winged petiole, with broad clasping base, green, paler beneath, sparsely setuliferous on both sides with yellow glandless setules; lower cauline leaves similar, base amplexicaul, round-auriculate, upper ones reduced, bractlike; stem arcuate or sinuately erect, branched only near top or remotely 3–5-branched beginning near base, lower branches long, 2–3-foliate, like terminal axis paniculate-corymbiform with 2–4 heads, terete and striate like stem, which is densely and finely setulose near base and sparsely canescent-tomentulose above, especially at bifurcations, or glabrate; peduncles 1.5–4.5 cm long, finely and sparsely canescent-tomentulose, becoming thickened and sulcate near base of head; heads erect, 50–100-flowered; involucre cylindric, 9–11 mm high, 4–5 mm wide at middle, remaining erect at maturity or partly reflexed, canescent-tomentulose; outer bracts 13–17, unequal, longest $\frac{1}{2}$ – $\frac{2}{3}$ as long as inner ones, outermost triangular or ovate, acute or acuminate, innermost lanceolate, acute or acuminate; inner bracts 20–24, lanceolate, gradually attenuate to the acuminate ciliate apex, with dark median dorsal line, becoming carinately spongy-thickened, sparsely and finely canescent-tomentose, sometimes pubescent with pale short gland hairs, ventrally glabrous; receptacle alveolate-fimbriate, alveoles 4–5-sided, 0.4–0.5 mm wide, fimbriae 0.05–0.4 mm high, glabrous; corolla 9–10 mm long; ligule 1.25 mm wide; teeth 0.2 mm long, obtuse; corolla tube 2–3 mm long, like lower half of ligule densely white-pubescent; anther tube about 3.8×1.25 mm dis.; appendages 0.6–0.7 mm long, acuminate, partly united; filaments 0.7 mm longer; style branches 1.25 mm long, slender, yellow; achenes reddish-brown, 4–5 mm long, 0.4–0.6 mm wide at middle, \pm incurved and laterally compressed, gradually attenuate to both ends, not expanded at the narrow (0.25 mm wide) summit, constricted above the callosed hollow base, 10–11-ribbed, ribs broad, rounded, glabrous or finely spiculate; pappus 5–6 mm long, white, straight, fine, caducous. Flowering Apr.–May; flowers yellow. Chromosomes $2n = 12$.

Hieraciodes hierosolymitanum O. Kuntze, Gen. 1: 346. 1891.

Palestine, from Idumea to Transjordan and Upper Galilee; S.W. Syria; Cyprus. Wadies, rock slopes, and shady places up to 1600 m. Type locality as given by Boissier, "in rocky places among hills around Jerusalem, particularly among rocks at the middle of the valley, Hinnom." This species is frequently mistaken for *C. montana* Urv., and the statements of Post (153) and Bouloumoy (Fl. Liban, Syrie, 215. 1930 sub syn. *C. Sieberi* Boiss.) to the effect that *C. montana* occurs in Lebanon and Palestine almost certainly refer to *C. hierosolymitana*.

Monomorphic.

Palestine: Idumea, rocky places near Hebron, 818 m, *Kotschy 626* (Bo, B); Judea, around Jerusalem, among rocks in Hinnom Valley, *Boissier* in 1846 (Bo) type; Judea, Jerusalem, rocky places, *Meyers and Dinsmore 3616A* (Minn); Judea, near Jerusalem, Deir es Scheikh, shady places, *Zohary* in 1931 (UC); Transjordan, Gilead, Wadi Waran, *Eig* in 1927 (HU, UC); Transjordan, Aman, rocks, *Eig* in 1929 (HU, UC); Samaria, Mt. Carmel, near Haifa, *Eig* in 1923 (HU); Samaria, Plain of Esdraelon, Tel Joseph, slopes of Gilboa (HU); Upper Galilee,

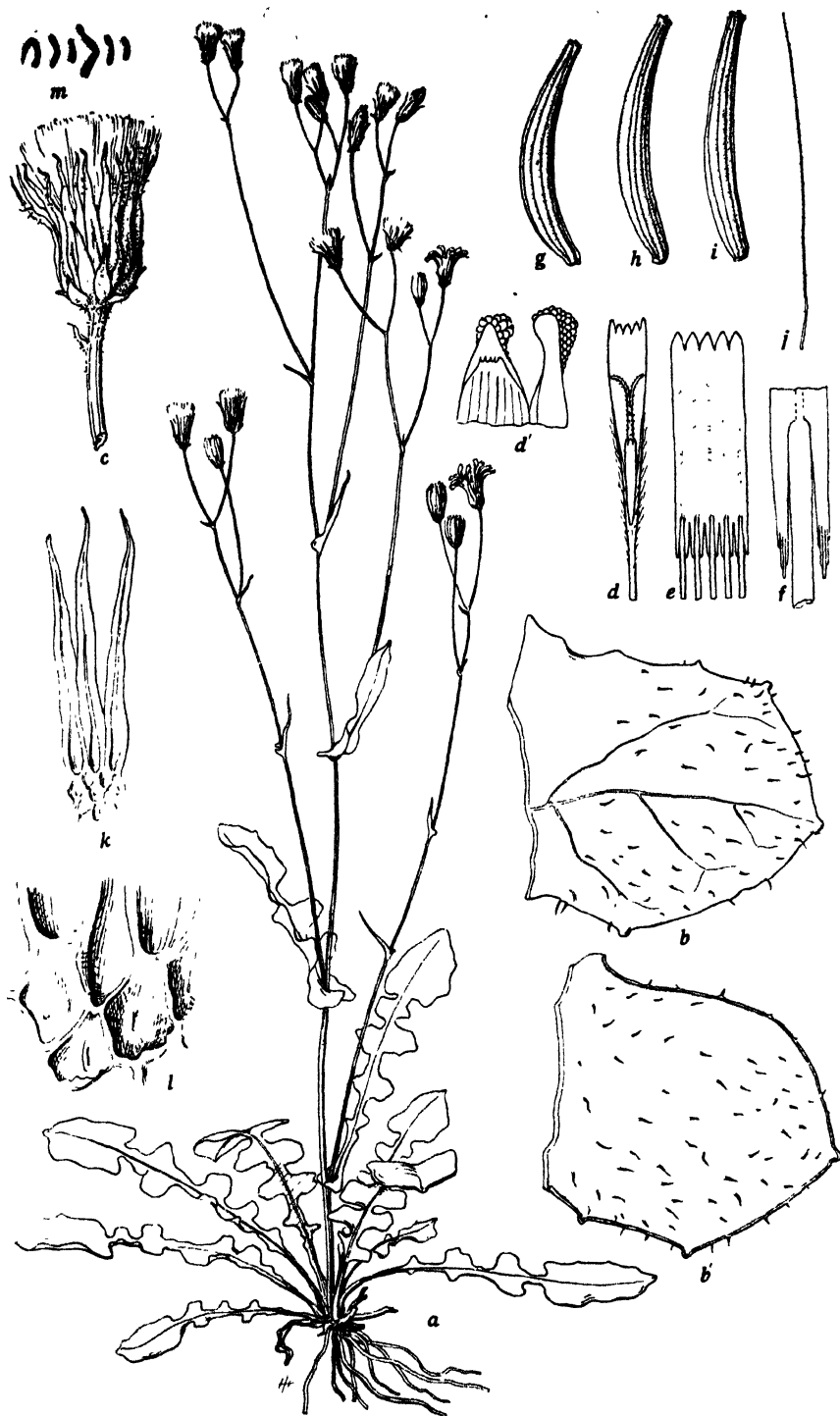


Fig. 38. *Crepis hierosolymitana*, a-j, from type (Bo); k-m, from hort. genet. Calif. 2619 (UC 466655): a, plant, \times ca. $\frac{1}{2}$; b, b', lateral lobes of caudical leaves, upper and lower sides, \times 4; c, mature head, \times 2; d, floret lacking ovary, \times 4; d', details of 2 ligule teeth, \times 25; e, anther tube, \times 8; f, detail of appendages, \times 32; g-j, 3 achenes and a pappus seta, \times 8; k, 3 inner bracts and adjacent receptacle, \times 8; l, detail of receptacle, \times 25; m, somatic chromosomes, $n = 6$, \times 1250.

Kefar Gileadi, *Smoly* in 1925 (HU). Syria: Lebanon, around Yaiola, *Samson 174* (Bo); Lebanon, cultivated field near first hill between Baramie and Lalalie, *Gaillardet 2033* (Bo). Cyprus: Mt. Olympus (Troodos), 1600 m, *Miss Topali* in 1931 (UC); Mt. Troodos, 1515-1818 m, *Haradjian 464* (DL); environs of Rizokarpaso, 100-150 m, *Haradjian 146* (DL).

Relationship

Crepis hierosolymitana is close to *C. montana* but is very distinct in the larger, more strongly ribbed achenes, yellow style branches, and much smaller florets, and especially in the usually more robust, taller stems. The brown wool of the caudex, which was supposed to be distinctive of *C. montana*, is very variable in both species, but is more often absent in *C. hierosolymitana*. Leaf shape is also variable in both species, but in *C. hierosolymitana* the lateral segments are always remote. Close also to *C. willemetioides*, but the latter is very distinct in leaf shape, horizontal rhizome, ciliate receptacle, and more finely ribbed achenes.

22. *Crepis montana* Urv.

Enum. Pl. Archipel., in Mem. Soc. Linn. Paris, 1: 101. 1822, non Reichb. (Fig. 39.)

Perennial, 2-3.5 dm high; rhizome vertical or curved, praemorse, 1-3 cm long, 0.5-0.8 cm wide, bearing strong fleshy fibers; caudex very short, leafy, usually bearing brown wool at base of leaves; leaves pubescent on both sides with pale glandular or glandless setiform hairs; caudical leaves 6-9, ascending, 5-22 cm long, 1.3-5.2 cm wide, oblanceolate, lyrate-pinnatifid, terminal segment broadly ovate, cordate, obtuse or acute, entire or remotely denticulate, lateral segments close or remote and then sometimes with smaller secondary segments interspersed, rounded or angular, obtuse or acute; cauline leaves few, lowest similar to caudical ones or sessile, middle and upper much reduced or bractlike; stems 1-4, erect, slender, striate, glabrous or pubescent, remotely 1-5-furcate, lower branches elongated, 1-7-headed, inflorescence a compound corymbiform cyme; peduncles 1.5-7 cm long, slender, arcuate, little if at all thickened at base of head, densely pubescent with short fine gland hairs, glands brown or black; heads medium, erect, about 25-flowered; involucre cylindric-campanulate, 9-10 mm high, 4-5 mm wide at middle in fruiting heads, \pm canescent-tomentose and gland-pubescent, ultimately reflexed; outer bracts 10-12, very unequal, longest $\frac{1}{4}$ - $\frac{1}{2}$ as long as inner ones, lanceolate, acuminate or acute; inner bracts 16-20, in 2 series, narrowly lanceolate, acuminate, dorsally keeled, spongy-thickened near base, ventrally glabrous; receptacle areolate-fimbriate, fimbriae low, glabrous; corolla 13.5 mm long; ligule 2 mm wide, teeth very unequal, 0.5-2 mm long in marginal florets; corolla tube 3.5 mm long, slender, densely pubescent with hyaline acicular hairs 0.3-0.5 mm long; anther tube 3.75×1 mm dis.; appendages 0.8 mm long, lanceolate, acute or furcate; filaments 0.5 mm longer; style branches 1.5-1.8 mm long, 0.1 mm wide, attenuate, green; achenes dark brown, 3-5 mm long, fusiform, terete or subterete, \pm curved, shortly attenuate below the scarcely expanded white pappus disk, abruptly constricted above the small hollow base, 15-20-ribbed, ribs narrow (up to 0.15 mm wide), smooth, equal or sometimes alternate ones narrower; pappus white, about 5 mm long, 2-seriate, fine, soft, caducous. Flowering Apr.-May; flowers yellow, with no red on outer face of ligule. Chromosomes, $2n = 12$.

Crepis Fraasii Sch. Bip., Flora 25: 173. 1842.

C. Sieberti Boiss., Diag. Pl. Orien. Nov. ser. 1, 11: 53. 1849, incl. syn.

Greece, from Thessaly and Corfu to the Peloponnesus, in mountains from 300 to 1300 m alt., on rocky slopes among trees and shrubs. The type locality, "montibus insulae cos," and Scarpanto (= Karpathos) are the only stations in the archipelago



Fig. 39. *Crepis montana*, a, a', from type (DC); b and g-i, from *Guiol* in 1930 (UC 429486); c and n-q, from *Demades* in 1921 (UC 313873 = hort. genet. Calif. 1175); d-f and k-m, from *Babcock 328* (UC 489436): a, a', leaf and flower stem, $\times \frac{1}{2}$; b, c, plants, $\times \frac{1}{2}$; d, head, $\times 2$; e, 2 adjacent inner involucre bracts, outer face, $\times 4$; f, detail of receptacle, $\times 25$; g, floret lacking ovary, $\times 4$; h, anther tube, $\times 8$; i, detail of appendages, $\times 32$; k-m, 2 achenes and a pappus seta, $\times 8$; n-p, 2 achenes and a pappus seta, $\times 8$; q, somatic chromosomes, $n = 6$, $\times 1250$.

known to the author. These islands are off the coast of S.W. Asia Minor, near Rhodes. Hence, it would seem not unlikely that this species would also occur on the mainland of Asia Minor. Dinsmore (*in Post*, 153) cites specimens of this species (not seen by me) from Lebanon and Palestine. Certain other specimens reported under synonyms from Lebanon, however, are almost certainly *C. hierosolymitana*, a closely related and superficially similar species. *C. montana* apparently does not occur in Crete. The specimen labeled *C. interrupta* Sm., in Herb. DC. Prod. ex Sieber Herb. Cretica 182b, is *C. montana* and was collected on Cape Malea, the southeastern promontory of Laconia. As Malea Bay is in Crete, an error in referring this specimen to Crete could have been made very easily. Reports of this species in Cyprus appeared to be based on confusion with *C. hierosolymitana* until the specimen cited below was seen. Even then, some doubt remained, since the place, Galata, cited by the collectors might be either a misspelling of Galatia, a town or village in N.E. Cyprus, or one of the places named Galata in Greece or Turkey at which they may have stopped while en route to Cyprus.

Greece: Archipelago, Cos (= Kos ?) I., summit, meadow or plain, *d'Urville* 130 (DC) type; Karpathos I., Mt. Lastros, *Pichler* in 1883 (US); Attica, Mt. Patera, *Heldreich* 2277b (US); Attica, Mt. Parnes, among *Abies*, *Heldreich* in 1854 (B); *ibid.*, 1100 m, *Demades* in 1921 (UC); *ibid.*, *Guiol* in 1930 (UC); Mt. Parnes, Mola, *Guiol* 314 (UC); Attica, Mt. Pentelicon, 300–900 m, among shrubs and trees, *Heldreich* 1050 (Ms, Bur); Attica, Argolis, or Laconia, Elymettas (?), *Sprunner* (Bo); Laconia, Cap Maleca (= Cape Malea), *Sieber*, Herb. Cretica 1826 (DC); Laconia, trail to Mt. Taygetos, 1300 m, *Babcock* 328 (UC); Zante I., *Margot* in 1837 (DC); Phthiotis, Patadjik (= Hypati) ex Herb. Sch. Bip. *Fraas* *missit*, 1841 (PC); Thessaly, Mt. Pelion, E. base, *Heldreich et Holzmänn* in 1883 (Bur); Thessaly, Mt. Olympus (?) reg., Lengada Pass, 1090 m, *Costopulos* in 1932 (UC); Corfu I., plateau of Mt. Pantocrator, *Bicknell* in 1891 (Ms). **Cyprus (?)**: vineyard near Galata (= Galatia, a town or village in Cyprus ?) "iter cyprium," *Sintenis et Rigo* in 1880 (K).

This species, like its close relative *C. Mungierii* of Crete, exhibits striking variations in size, especially in the leaves, which are also modified somewhat in form under widely different conditions. The plants shown in fig. 39 illustrate this observation. The type specimen and *Guiol*'s plant undoubtedly come from moist shady places, whereas the plant of *Demades*, from the same mountain as *Guiol*'s plant, must have grown in a dry exposed place. But neighboring plants of a single culture (from one original source) grown in the genetics garden exhibit marked variations in size of plant, including the leaves. Some of these variations are doubtless genetic, as are also such differences in size of achenes as those illustrated in fig. 39.

Relationship

Comparative morphology reveals close relationship between *Crepis montana* and 3 others, viz., *C. Mungierii*, *C. hierosolymitana*, and *C. willemetoides*. Indeed, the superficial resemblance between them is so great as to cause considerable difficulty for the casual observer, yet critical comparison reveals numerous distinctions. Furthermore, the chromosomes of all 4 of them exhibit very definite differences, even though the number is the same. These 4 species, as determined from both gross morphology and chromosome morphology, are less closely related to *C. lapsanoides*, *C. lyrata*, and *C. mollis*.

23. *Crepis Mungierii* Boiss.

Diag. Pl. Orien. Nov. ser. 1, 11: 55. 1849. (Fig. 40.)

Perennial, 0.6–2.4 dm high; rhizome very short, vertical, praemorse, bearing strong fleshy fibers; caudex short, leafy, bearing brown wool at base of leaves; leaves pubescent on both sides with pale glandular or glandless setiform hairs; caudical leaves 9–12, ascending, 3–14 cm long, 0.8–3.8 cm wide, oblanceolate, lyrate-

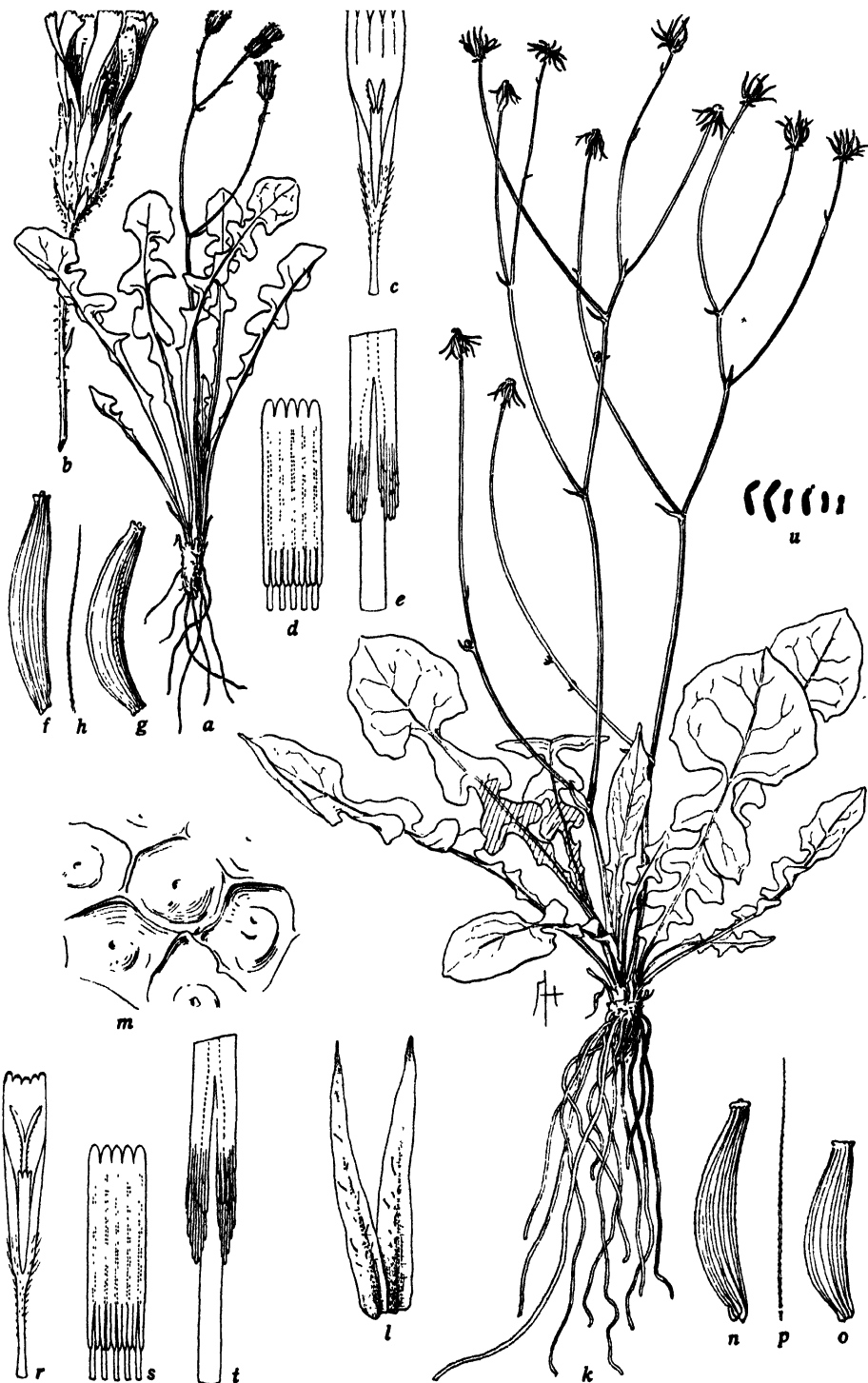


Fig. 40. *Crepis Mungierii*, a-h, from Babcock 315 (UC 429360); k-t, from Babcock 306 (UC 429382); u, from Babcock 314 (roots, hort. genet. Calif. 2877): a, plant, $\times \frac{1}{2}$; b, head, $\times 2$; c, floret lacking ovary, $\times 4$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f-h, 2 achenes and a pappus seta, $\times 8$; i, 2 adjacent inner involucre bracts, outer face, $\times 4$; m, detail of receptacle, $\times 25$; n-p, 2 achenes and a pappus seta, $\times 8$; r, floret lacking ovary, $\times 4$; s, anther tube, $\times 8$; t, detail of appendages, $\times 32$; u, somatic chromosomes, $n = 6$, $\times 1250$.

pinnatifid, terminal segment broadly ovate, cordate, obtuse, remotely denticulate, lateral segments remote, without secondary segments, semicircular or oblong-rounded or angular, obtuse or acute; cauline leaves few, sessile, lowest ones oblanceolate or lanceolate, dentate or denticulate, acute or obtuse, middle and uppermost much reduced or bractlike; stems 1-4, flexuous, becoming erect at maturity, slender, striate, glabrous or pubescent, simple or remotely 1-4-furcate and 1-6-headed;

TABLE 13
SYNOPTICAL COMPARISON OF THE CHARACTERS DISTINGUISHING *CREPIS MONTANA*
FROM *C. MUNGIERII*

Character	<i>C. montana</i>	<i>C. Mungierii</i>
Caudical leaves	5-22 cm long, usually wider, terminal segment obtuse or acute, lateral segments close or remote, with secondary segments	3-15 cm long, usually narrower, terminal segment always obtuse, lateral segments always remote, without secondary segments
Stems	2-3.5 dm high, erect, remotely 1-5-furcate, lower branches elongated, 1-7-headed	0.6-2.4 dm high, flexuous, ascending or erect at maturity, simple or 1-4-furcate, whole stem 1-6-headed
Aggregate inflorescence	a many-headed compound corymbiform cyme	an irregular few-headed corymbiform cyme
Heads	about 25-flowered	35-50-flowered
Corolla	about 13 mm long	about 10 mm long
Ligule	yellow, without red on outer face	yellow, with red on outer face
Ligule teeth	very unequal, 0.5-2 mm long	nearly equal, 0.3-0.6 mm long
Anther tube appendages	0.8 mm long, lanceolate, acute or furcate at tip	0.6-0.8 mm long, oblong, acute, obtuse or truncate
Style branches	1.5-1.8 mm long, green	about 1.25 mm long, yellow or sometimes greenish
Achenes	3-5 mm long, 15-20-ribbed, ribs wider, smooth	3-3.75 mm long, about 15-ribbed, ribs narrower, finely spiculate
Pappus	about 5 mm long	3-4 mm long
Distribution	Greece	Crete

peduncles 2-9 cm long, very slender, arcuate, canescent-tomentulose, sometimes pubescent with short gland hairs near base of head, glands brown or black; heads medium, erect, 35-50-flowered; involucre cylindric-campanulate, 9-10 mm high, 4-5 mm wide near base in fruiting heads, \pm canescent-tomentulose and pubescent with short glandular or longer glandless hairs, ultimately reflexed; outer bracts 10-12, unequal, longest $\frac{1}{4}$ - $\frac{1}{2}$ as long as the inner, lanceolate, acuminate or acute; inner bracts 12-14(18), in 2 series, lanceolate, acute, dorsally keeled and spongy-thickened near base, ventrally glabrous; receptacle areolate-fimbriate, fimbriae low, naked; corolla 10-13 mm long; ligule 1.5-2 mm wide; teeth 0.3-0.6 mm long; corolla tube 3-3.5 mm long, densely pubescent above with acicular hairs 0.3-0.4 mm long; anther tube about 3.5×1 mm dis.; appendages 0.6-0.8 mm long, oblong; filaments 0.4-0.5 mm longer; style branches 1.25 mm long, 0.1 mm wide, attenuate, yellow or sometimes greenish; achenes dark brown, 3-3.75 mm long, terete or subterete, \pm curved, shortly attenuate below the scarcely expanded white pappus disk,

abruptly constricted above the small hollow base, about 15-ribbed, ribs equal, very narrow (less than 0.1 mm wide), very finely spiculate under lens; pappus white, 3–4 mm long, 2-seriate, very fine, soft, caducous. Flowering May–June; flowers yellow, tinged red on outer face of ligule. Chromosomes, $2n = 12$.

Crete, mountains throughout the island from 900 m alt. up to some of the highest peaks (Volakia is about 2300 m), crevices of rocks in exposed or shady places, often abundant. Type locality, Mt. Ida, above Vorisa, 900–1200 m, among *Quercus* sp. Also Karpathos, on Mt. Lastros (see Pichler's spec. cited below).

Ecological variations are especially notable in this species. For example, there are shade forms which bear such striking resemblance to *C. montana* as to be easily mistaken for it (cf. fig. 40, *k*). The latter species, however, was not found in Crete by the author, but *C. Mungierii* was abundant. Garden cultures from seed collected from shade and low altitude forms of *C. Mungierii* were almost identical with cultures grown from high altitude forms. Apparently, there is less genetic variation in *C. Mungierii* than in *C. montana*.

The specimen of Pichler from Karpathos is the only collection known to me from outside Crete. It was filed under the label *C. Sieberi* var. *Mungierii* and *C. Mungierii* B. et H., with the type in Herb. Boiss. in 1925, at which time it was not realized that the locality given on the label was not in Crete. But a small photograph of the plant, taken at the time, shows that in size, habit, leaf shape, heads, and length of florets it corresponds closely with this species. Hence, it is practically certain that this species also occurs on Karpathos, but whether in an indigenous or adventive state is still uncertain.

Crete: W. reg., Canea-Sphakia, Omalo, *Reverchon* 256 (Bur); Omalo plain, cave of disappearing river near entrance to plain, about 1100 m, *Babcock* 306 (UC); Mt. Volakia, *Baldacci* 78 (Bur); Mt. Volakia, peak, 2300 m, *Babcock* 315 (UC); Imbros Gorge, *Babcock* 300 (UC); central reg., Mt. Ida, above Vorisa, 900–1200 m, *Heldreich* in 1846 (Bo, VM) type, isotype; Mt. Aphendi, among rocks, *Patten* K203 (G). **Karpathos:** Mt. Lastros, in a gorge, in shade, *Pichler* (Bo).

Relationship

Crepis Mungierii is very close to *C. montana* (*q.v.*), but is certainly distinct in chromosome morphology. Although the 2 species are very similar in external morphology, there are sufficiently distinct and constant differences to warrant their recognition as species. The more useful of these differences for taxonomic purposes are set forth in the accompanying synopsis (table 13).

SECTION 6. SOYERIA

Relationships of the Species

The 3 species of this section are characterized by a vertical woody elongated root, a rather stout stem or stems which are much longer than the basal leaves, one or few large or medium many-flowered heads, hairy involucres, with long outer bracts and the inner bracts little changed at maturity. They are all montane species and, except for *C. blattarioides*, mostly alpine or subalpine.

C. pontana, next to *C. sibirica*, is the most primitive 5-paired species in the genus, and it shows considerable resemblance to *C. sibirica* in both gross morphology and

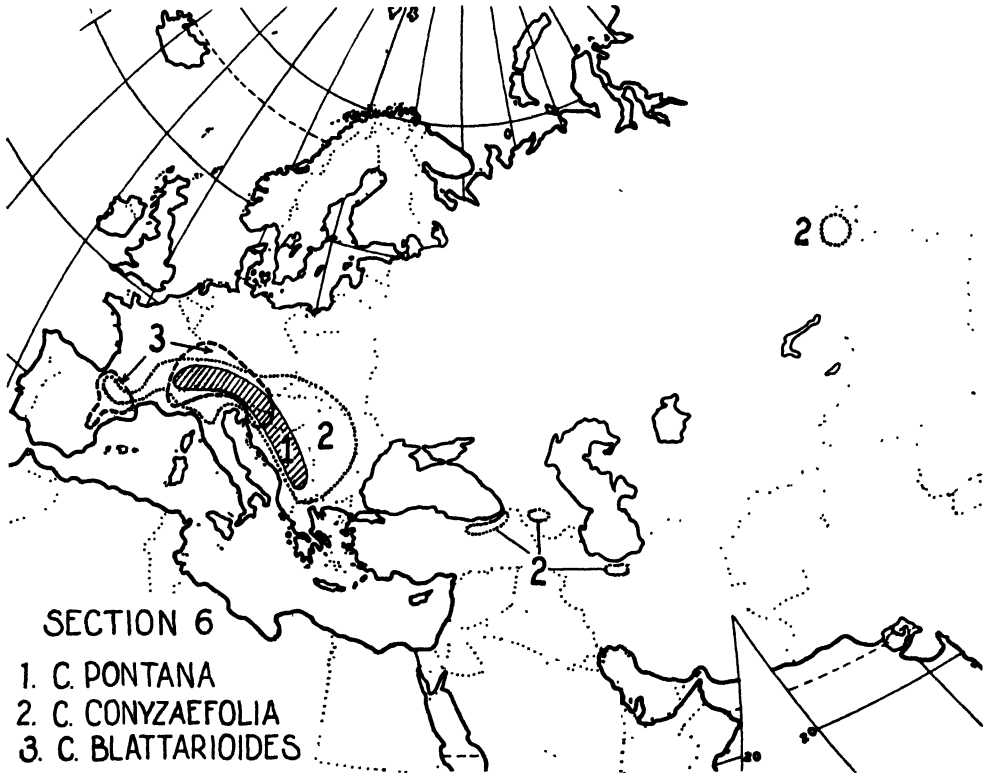


Fig. 41. Geographic distribution of the 3 species in sec. 6. The disjunct distribution of *C. conyzaefolia*, the most primitive 4-paired species in the genus, which extends all the way from the Altai reg. to the Pyrenees, is of great significance for the hypothesis that the genus originated in Central Asia. Based on Goode Base Map No. 201 PC. By permission of the University of Chicago Press.

karyotype. But its long vertical root and the pubescence on the inner face of the involucral bracts connect it with the other species of this section. *C. pontana* is restricted to the European Alps from Switzerland to the N. Balkan Pen.

C. conyzaefolia is the most primitive 4-paired species in the genus. Morphologically, it is closer to *C. pontana* than *C. blattarioides*, also it is closer to *C. pontana* than *C. alpestris* or any other species of sec. 8. Furthermore, the karyotype is more like that of *C. pontana* than those of the other species mentioned. It is possible, therefore, that *C. pontana* is the present-day representative of the original stock from which all the deep-rooted 4-chromosome species descended. *C. conyzaefolia* has the widest distribution of any species in the section, its distribution being from the Pyrenees to N. Persia and the Altai reg. Thus, it is one of the few more primitive

species with a discontinuous distribution extending all the way from the assumed center of origin of the genus to the Pyrenees (see fig. 41). In this connection its morphological resemblance to *C. alpestris* (q.v.) is of special interest.

C. blattarioides is very distinct from the other species in this section in habit and leaf shape, and its karyotype is more like that of *C. alpestris* and other species of sec. 8. But in floral and achenial characters it is much closer to *C. pontana* and *C. conyzaeifolia*, and such resemblance is considered of greatest significance. *C. blattarioides* is restricted in distribution to the mountains of S.W. and S. central Europe.

Key to the Species of Section 6

- Lower leaves oblong or elliptic; marginal florets about 25 mm long; achenes 10–12 mm long. 24. *C. pontana*, p. 295
- Lower leaves oblanceolate; marginal florets 18–23 mm long; achenes 5–9 mm long.
- Caudical leaves persisting; longest outer involueral bracts $\frac{1}{2}$ – $\frac{2}{3}$ as long as the inner; inner bracts 12–24, pubescent on inner face; corolla tube pubescent. 25. *C. conyzaeifolia*, p. 297
- Caudical leaves disappearing early; outer involueral bracts nearly equal to the inner; inner bracts 10–12, glabrous on inner face; corolla tube glabrous. 26. *C. blattarioides*, p. 302

24. *Crepis pontana* (L.) Dalla Torre

Anleit. Beob. Alpenreisen, 259. 1882. (Fig. 42.)

Perennial, 1.5–6 dm high; root elongated, straight, woody, 4–6 mm wide; caudex 1–2 cm long, 6–10 mm wide, covered with brown bases of old leaves; caudical leaves 2–4, ascending, 4–12 cm long, 1.5–3 cm wide, oblanceolate, acute, narrowed at base into a short broadly winged petiole, sinuately or retrorsely denticulate, glabrous except short glandless hairs along veins beneath; lower cauline leaves 2–3, equal to or larger than caudical leaves, oblong, obtuse-mucronate, sessile, subamplexicaul or cordate-amplexicaul, dentate; middle and upper cauline leaves remote, lanceolate, acuminate, entire, uppermost bractlike; stem simple, 1-headed, rarely 2-headed, 2–4 mm wide at base, erect, elongated, striate, sparsely canescent-tomentulose, near base of head thickened, tomentose, hairy; head erect, large, 3–5 cm wide in anthesis, many-flowered; involuere broadly campanulate, densely hirsute with long green or yellowish glandless hairs; outer bracts 12–15, very unequal, longest $\frac{2}{3}$ – $\frac{3}{4}$ as long as inner bracts, acute or acuminate; inner bracts about 25, up to 20 mm long, lanceolate, or innermost linear, acuminate, densely pubescent on upper half of inner face with short white hairs, becoming indurate but not much changed in fruit; receptacle areolate or alveolate, with occasional white hairs 0.5–1 mm long between the areoles; corolla 25 mm long; ligule 2.5 mm wide; teeth 0.6–0.8 mm long, oblong; corolla tube 8 mm long, glabrous; anther tube 5.75×1.5 mm dis.; appendages 0.8 mm long, oblong, truncate; filaments stout, 1.5–2 mm longer; style branches 3 mm long, 0.2 mm wide, gradually attenuate upward, yellow; achenes tawny, brown at apex, 10–12 mm long, 1.5–2 mm wide, columnar, \pm angled, strongly attenuate to the narrow apex, without expanded pappus disk, constricted above the narrow pale-calloused base, about 17-ribbed, ribs unequal, with 5 or 6 stronger ones, rounded, smooth; pappus pale tawny, 9 mm long, 3–4-seriate, setae brittle, mostly strong, with a few outermost shorter and finer, persistent. Flowering July–Aug.; flowers yellow. Chromosomes, $2n = 10$.

Hypochaeris pontana L., Sp. Pl. ed. 2. 1140. 1763.

Andryala pontana Vill., Hist. Pl. Dauph. 3: 67, t. 23. 1789.

Hieracium montanum Jacq., Fl. Aust. 2: 54, t. 190. 1774.

Soyeria montana Monn., Ess., 75. 1829.

Crepis montana Tausch, Flora 11: 79. 1828, non Urv.

Hieraciodes pontanum O. Kuntze, Gen. 1: 345. 1896.

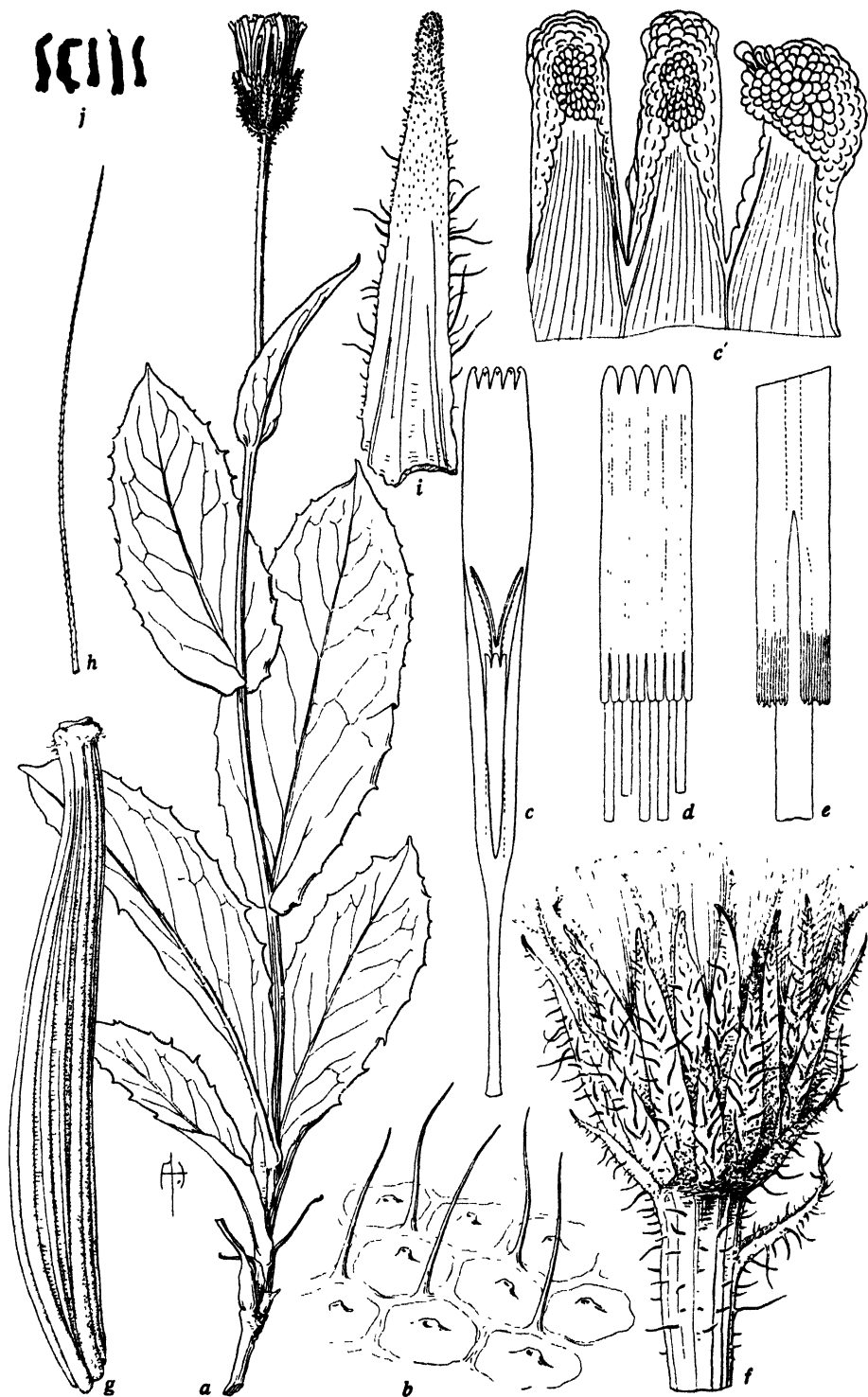


Fig. 42. *Crepis pontana*, a-f, from Leresche (Bo); g-j, from Beauverd (Bo); l, from hort. genet. Calif. 2204 (seeds received from Munich Bot. Gard. through Dr. M. Navashin): a, plant, $\times \frac{1}{2}$; b, detail of receptacle, $\times 25$; c, floret lacking ovary, $\times 4$; c', detail of ligule teeth, $\times 50$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, fruiting head, $\times 2$; g, h, achene and pappus seta, $\times 8$; i, inner involucre bract, inner face, $\times 4$; j, somatic chromosomes, $n = 5$, $\times 1250$.

European Alps from the high Jura southeastward to the W. Balkan Pen., in Bosnia, Hercegovina, and Montenegro, acc. to Markgraf (849). Although reported by Hegi (1138–1139) in the Balkan Mts. of Bulgaria and (dubiously) in the Carpathians, I have seen no specimens from either mountain range; and in Professor B. Stefanoff's list of Bulgarian species of *Crepis*, which he carefully prepared for me, it is not reported as occurring in that country. Its existence in the Carpathians therefore seems very doubtful. In alpine meadows, on stony slopes, and in sub-alpine forests it is sometimes abundant, but (acc. to Hegi, *loc. cit.*) usually scattered and seldom gregarious; mostly on calcareous formations, at elevations from 1200 to 2500 m.

Monomorphic, with some variations in shape and size of leaves and number of cauline leaves. The type of Linnaeus was not seen by me, but typical specimens, collected in 1832 and labeled *H. montanum* and *C. montana*, were found in Herb. DC. Prod. VII: 171 n. 54.

France: Le Galibir, 2300 m, *Faure* in 1898 (UC); la Salette, Isère, 2200 m, *Cuny* in 1911 (UC); massif de les Folliu, Les Fretes, *Beauverd* (Bo); Lautaret, *Pellat* in 1879 (Grenoble); la Grave, 1450 m, *Mathonet* in 1861 (Bur); Mt. Seuse au Fays, near Gap, *Billot* in 1853 (Bur); Savoie, Mt. Brezen, *Burnat* in 1846 (Bur). **Switzerland:** Jura, la Dôle, *Laguesse* in 1873 (K); *ibid.*, *Muret* (Bur); Alpe de Crai, *Leresche* (Bo); le Davos, 1515 m, *Maritzi* in 1832 (DC); Valais, Maienwand, *Burnat et al.* in 1915 (Bur). **Austria:** Carinthian Alps, near Heiligenblut, *Hoppe* in 1832 (DC); central Tirol, *Kerner* in 1872 (Fl); Austria ? "auf der Plecken," in 1864 (K); Pusteria, Sexten, Kreuzberg Mts., 1515–1818 m, *Huter* in 1871 (K).

Relationship

Crepis pontana shows considerable resemblance to *C. sibirica* in leaves, habit, involucre, florets, and achenes, as well as in karyotype. But it differs strikingly in the long, vertical taproot and the usually 1-headed stem, and the inner involucre bracts are pubescent on the inner face, as in *C. conyzaefolia*. *C. pontana* therefore stands as a connecting species between other *Crepis* species, with deeply penetrating taproots, and *C. sibirica* and its nearest relatives.

25. *Crepis conyzaefolia* (Gouan) Dalla Torre

Anleit. Beob. Alpenfl. 145. 1884. (Pl. 4. Fig. 43.)

Perennial, 1.2–5 dm high, root straight, woody, 2–6 mm wide; caudex 1–2 cm long, 5–10 mm wide, covered with brown bases of old leaves; caudical leaves numerous, ascending, 5–30 cm long, 1–4(5) cm wide, oblanceolate, acute or obtuse, narrowed toward base into a broadly winged petiole, runcinately denticulate, dentate or pinnatifid, rarely pinnately parted with remote narrow unequal lobes, pubescent with short pale fine or very fine glandless hairs, sometimes \pm glandular, rarely glabrescent; lower cauline leaves 1–3, remote or congested near base, oblanceolate or lanceolate, broadly petiolate or sessile, dentate or denticulate, pubescent, middle leaves 1–4, gradually reduced, oblong or lanceolate, amplexicaul, sagittate-auriculate, uppermost leaves bractlike, sometimes densely gland-pubescent or villous; stem erect, robust, rather woody, sulcate, pubescent with yellow glandless hairs and/or short gland hairs, rarely glabrescent, shortly 1–9-branched above middle, or sometimes branched from near base, the lower branches elongated, rarely simple and 1-headed but \pm leafy or bracteate, branches pedunculate or rarely with 2 or more heads, arcuate, often densely pubescent, not much thickened or sometimes constricted near head; heads erect, large, 2–4 cm wide in anthesis, many-flowered; involucre broadly campanulate, 10–16 mm high, very dark green, sometimes paler, \pm hirsute with greenish or yellowish glandless hairs intermixed with shorter gland hairs, sometimes \pm canescent-tomentose, rarely glabrescent; outer bracts about 10

with 2 or 3 more subtending ones, unequal, longest $\frac{1}{2}$ as long as inner bracts, lanceolate or linear, obtuse or acute; inner bracts 12–24, lanceolate, acute or obtuse, white-ciliate at apex, pubescent on inner face with rather coarse white hairs, these sometimes few or inconspicuous, becoming indurate but otherwise not much changed in fruit; receptacle alveolate-fimbriate, alveoles 0.5–0.75 mm wide, fimbriae unequal, very shortly ciliate; corolla 18–21 mm long; ligule 2.5 mm wide; teeth 0.25–0.9 mm long; corolla tube 5–7 mm long, pubescent with coarsely stalked navicular or acicular hairs 0.05–0.4 mm long arranged singly or in groups; anther tube (5.25)6 \times 1.25 (1.5) mm; appendages 0.8–0.9 mm long, oblong, truncate or obtuse; filaments 0.75–1 mm longer; style branches 3–3.75 mm long, 0.15 mm wide, attenuate, yellow; achenes tawny, 5–9 mm long, 1–1.25 mm wide, subterete, fusiform, nearly equally attenuate to both ends or more strongly so upward, with slightly expanded pappus disk, definitely constricted near the narrow calloused base, 15–20-ribbed, ribs narrow, rounded, smooth; pappus white or pale yellowish, 5–9 mm long, 2–4 seriate, unequal, outer setae finer, coarsest 50 μ wide at base, united at base, strongly persistent. Flowering July–Aug.; flowers yellow. Chromosomes, $2n = 8$.

Hieracium conyzaefolium Gouan, Illus. Bot. 59. 1773.

H. conyzoides Lamk., Fl. Fr. 2: 197. 1778.

H. grandiflorum All., Fl. Ped. 217, t. 29. 1785.

H. intybaceum Lamk., Diet. 2: 369. 1786.

H. pappoleucum Vill., Hist. Dauph. 3: 134. 1789.

Crepis grandiflora Willd., Enum. Pl. Suppl. 56. 1813.

Lepicaune intybacea Lap., Abr. Pyr. 479. 1813.

L. grandiflora Lap., loc. cit.

Crepis grandiflora Tausch, Flora 11: 80, 1828.

Soyeria grandiflora Monn., Essai, 76. 1829.

Brachyderea grandiflora Sch. Bip., Cich. no. 420. 1841.

Crepis djimilensis C. Koch, Linnaea, 23, 683. 1850.

C. pontica C. A. Mey., Mem. Acad. Petersb. ser. 6, Sc. Nat. 7: 14. 1850.

C. orbelica Velen., zvlastni ostik Vestnika, p. 2, 52. 1890.

Hieraciodes conyzifolium O. Kuntze, Gen. 1: 345. 1891.

C. balcanica Velen., op. cit., 53.

C. trojanensis Urum., Oestr. Bot. Zeits. 49: 202. 1899.

C. conyzifolia subsp. *grandifolia* (Tausch) Domin, et subsp. *confusa* (Woloszczak) Soó ex Domin in Plant. Cechoslov. Bot. Enum., Preslia (Vest. Ceskoslov. Bot. Spol. Praze) 13–15: 251. 1935. Spec. of the last not seen by me, but see below, under minor variants.

S. Europe, from the Pyrenees to the Balkan Pen. and Carpathian Mts.; W. Asia in N. Asia Minor, Transcaucasia, N. Persia (acc. to Bornmüller, Bull. Herb. Boiss. ser. 2, 7: 434. 1907) and the Altai reg.; subalpine or alpine, most frequently in meadows below timber line, but occasionally above the limit of forests. Usual altitudinal range from 1000 to 2000 m, but reported as low as 600 m and as high as 3000 m. Acc. to Braun-Blanquet and Rübel (1486), in the middle E. Swiss Alps this species occurs on soils deficient in lime, including schists, and is found mostly on sterile meadows in dry sod of *Festucetum* and *Nardion*. But in the Pyrenees it has been found on a granitic substratum (see first specimen cited below). Acc. to Pax (1:197, 211; 2:211 *et seq.*), *C. conyzaefolia* (as *C. grandiflora*) is abundant at many localities in the W. and E. Carpathian Mts., occurring in open swampy woods at elevations lower than subalpine, also in subalpine and alpine meadows (cf. Adamovic, 367).

The type of Gouan was not seen by me, but in the Herbarium of the National Museum of Prague I saw a specimen of Tausch, n. 916, labeled "*C. grandiflora* W. (*Hierac.* All.)," which is the usual form of this species.

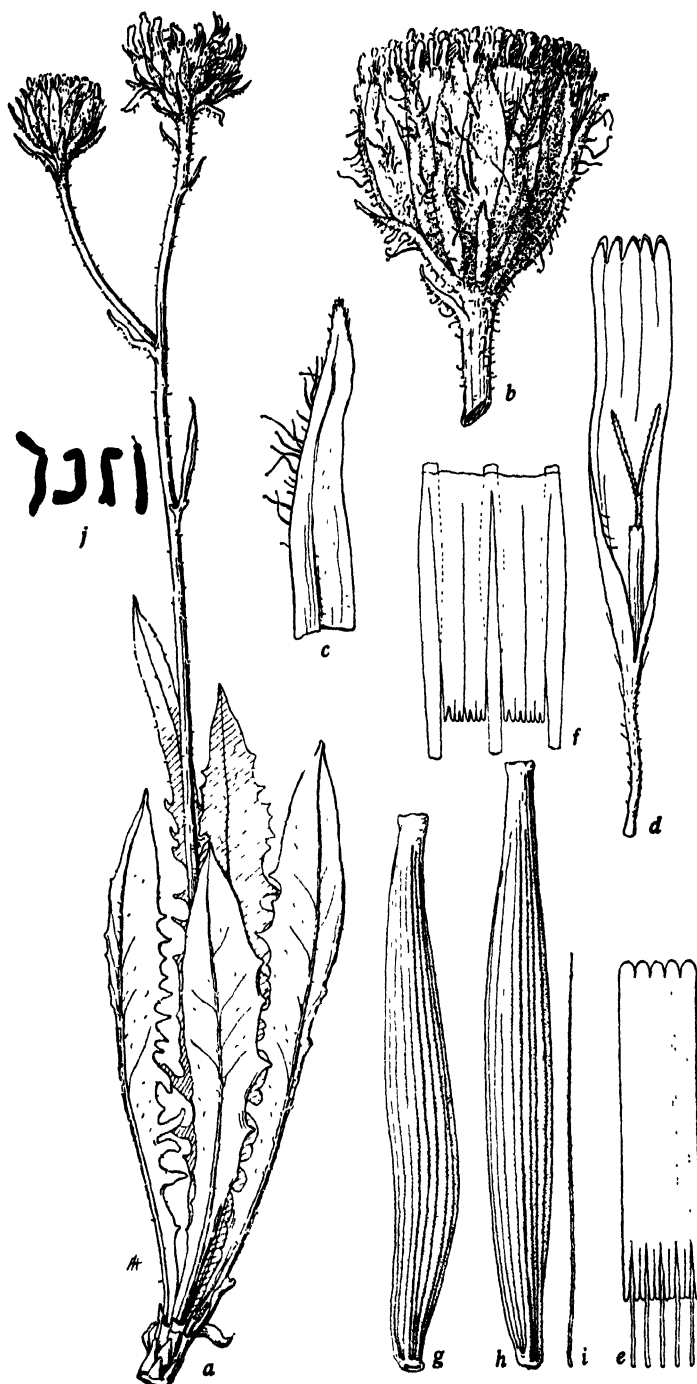


Fig. 43. *Crepis conyzacifolia*, a-f, from Valpius in 1887 (UC 65605); g-i, from Hoppe in 1832 (DC Prod. 7: 166, n. 30); j, from hort. genet. Calif. 2183 (seeds received from Lausanne Bot. Gard. through Dr. M. Navashin): a, plant, $\times \frac{1}{2}$; b, head, $\times 2$; c, inner involucre bract, ventral side, $\times 4$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g-i, 2 achenes and a pappus seta, $\times 8$; j, somatic chromosomes, $n = 4$, $\times 1250$.

Spain: Pyrenees, La Cerdana, Vallée de Carol, Porta, granitic detritus, *Sennen 2727* (Bur, UC). **France:** Pyrenees, between Mont Louis and Lake Bouillouse, *Babcock 396* (UC); Basses Pyrenees, near Eaux Bonnes, *J. Ball* in 1861 (Minn); Ariège, Orlu, *Guilhat* in 1898 (Bur); Cantal, near Lacrouz, *Puyfol* in 1884 (Bur); Plomb du Cantal, Forêt du Lioran, *Gaudefroy* in 1878 (K); Hautes-Alpes, Lautaret, *Faure 2523* (K, Ms); Savoie, Mt. Jovet, *Mouillefarine* in 1897 (Po). **Switzerland:** Valais, Mt. Blasenhorn, *Lagger* in 1843-1844 (Bur); Engadin, *Valpius* in 1887 (UC); Upper Engadin, Pontresina, *Mayer* in 1895 (UC); Tessin, Cortacio, *Chenevard* in 1902 (DL). **Italy:** Alpes Maritimes, Madonna delle Fimrenti (Bo); Longobardia, Sondrio, *Longa* in 1911 (Bur); Pedemont, Thermas Valderii, *Reuter* in 1852-1853 (K, PC). **Tirol:** southern, Zillertal Valley, *J. Ball* in 1871 (US); northern, Alpbach, Goltenberg, *Woynar* in 1887 (US, Minn); central, near Trins, *Kerner 3403*, (Bur, Minn); eastern, Pusteria, Villgraten, *Gander* in 1886 (UC). **Germany:** Bavaria, near Tegernsee, *Einsele 1498* (Po); *ibid.*, *Manzka* (Hayek); Rothenbuch, *Muller* in 1890 (Minn). **Austria:** Styria, Hohe Tauern, *Hayek* in 1911 (B, Bur); Carinthia, alpine, *Hoppe* in 1832 (DC). **German-Czechoslovakian Frontier:** Sudetic Mts., Kiesberg, *Häger* in 1879 (Bur); Riesen Mts., Melzergrund, *Woller* in 1901 (Po, Minn). **Hungary:** Mt. Craciunel, Rodman, *Degen* in 1902 (Po). **Carpathian Mts.:** Zawrad, *Bilimek* in 1855 (B). **Rumania:** Transylvania, Gorbati, *Richter* in 1898 (Po). **Bulgaria:** central Balkan Mts., Trojan dist., Kosetstena, *Urumoff* in 1898 (PV, VG, Sofia-M, UC) m.v. 1; central Balkan Mts., Mt. Murgas, *Urumoff* in 1903 (PV, Sofia-M, UC) m.v. 2; W. reg., Mt. Vitoscha, *Velenovsky* in 1889 (PV) m.v. 3; *ibid.*, *Stefanoff* in 1929 (UC) m.v. 3; S.W. reg., Mt. Rilo, *Velenovsky* in 1889 (PV) m.v. 4; Mt. Rilo, Demir Kapiga, *Stribrny* in 1915 (Sofia-M, UC) m.v. 4; Macedonian frontier, Belasitza Mts., near Demir Kapiga Pass, *Stojanoff* in 1920 (Sofia, UC) m.v. 5. **Bosnia:** Stolac plateau, *Visegrad* in 1897 (B). **Hercegovina:** near Kovčice, *Pantocsek* in 1872 (Bur). **Macedonia:** Mt. Ljuboten (?), *Adamovic* in 1901 (B). **Asia Minor:** Pontus, Gümüşchkhane, *Freyn 7194* (B) m.v. 6; Karagoellidagh, alpine pastures, *Sintenis 7194* (K) m.v. 6; Lazistan, Djimil, *C. Koch* (B) m.v. 6; Lazistan, Khabakar, *Balansa* in 1866 (P, K, Bo) m.v. 6. **Turkish-Transcaucasian Frontier:** Kartschal Mts. (southwest of Batum), Gratinca, 3000 m, *Rickmers 57* (B). **Transcaucasia:** Georgia (= Guria = Mingrelia), *Nordmann* (Lenin ex Herb. Ledeb.) m.v. 7. **Altai:** *Ledebour* (B) misit Ledeb. sub. *H. chrysanthum*.

Minor Variants of *C. conyzaeifolia*

As would be expected in a primitive species of such wide geographic distribution, numerous more or less distinct forms have been collected and some of these have been described as species. For the present, however, all of these have been reduced to the rank of minor variants (see below). It is not surprising also that within a given area, such as the Swiss Alps, the Tirol, or Bulgaria, numerous forms have been discovered and given varietal names, beginning with de Candolle's *Prodromus*. No effort has been made to assemble all these varietal names, which often refer to such minor characters as degree of dissection of the leaves and nature of the indumentum. The leaves may vary from denticulate to deeply runcinate-pinnatifid. An unusually vigorous specimen is shown in pl. 4.

The indumentum of the plant may be of 3 or sometimes 4 phases. The most constant phase consists of yellowish glandless hairs on the lower leaves and stem. Seldom are these entirely absent. Next are the shorter gland hairs often found on the upper stem and peduncles, but sometimes distributed more generally over the plant. Thirdly, the pubescence of the involucre may consist of long yellow glandless hairs, or these may be replaced by black glandless setules which may sometimes extend downward on the peduncles and uppermost leaves. In the fourth phase there are no yellow hairs on the involucre, the black setules are sparse and short, and there is more or less white tomentum which may extend onto the peduncle. This phase is characteristic of several Bulgarian forms (see m.v. 1-5). It is reminiscent of *Crepis alpestris*, but from the extensive lists of specimens in the 3 herbaria of Sofia, which were kindly prepared for me by Professor Dr. B. Stefanoff, it appears that, whereas there have been 35 collections of *C. conyzaeifolia*, *C. alpestris* is entirely absent from that region. Although it is considered a rare species, *C. conyzaeifolia* is widely distributed, at least in the western half of Bulgaria. The *C. alpestris*-like involucre of these Bulgarian forms cannot be explained as due to recent hybridization; but it is very probable that *C. alpestris* migrated from Asia Minor across Bulgaria in Tertiary times in order to reach the W. Balkan Pen. and the W. Carpathian Mts., and through hybridization with *C. conyzaeifolia* it may have impressed some characteristics on their present-day descendants. But, on the other hand, these peculiar Bulgarian forms may merely result from the potential variability of *C. conyzaeifolia*.

Natural hybrids, however, do occur between *C. conyzaeifolia* and at least 2 other species, *C. alpestris* and *C. blattarioides* (Bruegger, Jahresb. Nat. Ges. Graub. 2[23-24]: 110. 1880). Similar hybrids have doubtless been noted and even named by others. For example, in Gray Herb. is a

specimen collected by Borbás in the Velebit Mts. of Croatia, bearing a label *Crepis pseudo-blattarioides* Borbas, which combines certain leaf characters of *blattarioides* with involucreal characters of *conyzaefolia*. Furthermore, *C. conyzaefolia* var. *Degeniana* Borbás, ex Schinz u. Keller, Fl. Schweiz Krit. ed. 3, 360, 1914, ex descr., is probably a hybrid between *conyzaefolia* and some other species.

1. (*C. trojanensis* Urum., Oestr. Bot. Zeits. 49: 202. 1899.) Only 1.2–1.5 dm high and 1–3 headed; leaves small; peduncle and involucre canescent-tomentose; involucre 10 mm high, shortly pubescent with yellowish and dark green hairs. Urumoff in 1898 (Sofia, PV, UC), Kozetastena, Trojan dist., Balkan Mts., Bulgaria.

2. Caudical leaves deeply runcinate-pinnatifid; stem rather slender, glabrous, 2-headed; peduncles 5–6 mm long, canescent-tomentose near head; involucre 12 mm high, canescent-tomentose, inner bracts rather narrow, with short black hairs near the apex. Urumov in 1903 (Sofia, PV, UC), labeled *C. balcanica* Velen., but not corresponding to that form, Mt. Murgas, central Balkan Mts., Bulgaria.

3. (*C. balcanica* Velen., zvlstni otisk Vestnika, pt. 2, 53. 1890.) Stem usually branched from below middle; branches remote, long, arcuate, pedunculate; peduncle shortly pubescent and tomentulose near head; involucre 10–15 mm high, canescent-tomentose, \pm pubescent, with pale and/or dark hairs; achenes and pappus typical. Velenovsky in 1889 (PV), Mt. Vitoscha; Stefanoff in 1929 (Sofia, UC), subalpine meadows, 2000 m, Mt. Vitoscha, W. Bulgaria.

4. (*C. orbilica* Velen., zvlstni otisk Vestnika, pt. 2, 52. 1890.) Stem 2–8 dm high; cauline leaves sometimes not auriculate; peduncle and involucre fuscous-tomentose, densely pubescent with very short gland hairs and longer black glandless hairs; marginal achenes strongly curved; pappus 7–8 mm long. Velenovsky in 1889 (PV), near monastery, Mt. Rilo; Stribrny in 1915 (Sofia-M, UC); Stojanoff et Stefanoff in 1919 (UC), 2500 m, Mt. Rilo, S.W. Bulgaria.

5. (*C. grandiflora* var. *macedonica* Stoj. et Stef., in herb.) Only 1.2 dm high; leaves correspondingly small; stem branched from below middle, branches few, remote, rather short; cauline leaves and stem canescent-tomentulose; heads rather small; involucre canescent-tomentose and sparsely pubescent with short black hairs; style branches yellow; pappus white, 7 mm long, 2-seriate; achenes lacking. Stojanoff in 1920 (UC), near Demir Kapiga Pass, 1700 m, Belasitza Mts., frontier of Bulgaria-Macedonia.

6. (*C. djimilensis* C. Koch, Linnaea 23: 683. 1850; *Hieracioides djimilense* O. Kuntze, Gen. 1: 345. 1891.) Peduncle and involucre fuscous-tomentose and densely pubescent with short brown glandular and glandless hairs; involucre 12 mm high; florets, immature achenes, and pappus typical. C. Koch (B) Djimil, Lazistan; Freyn 7194 (B) Gümüşkhane, Pontus, Asia Minor. Also reported from N. Persia, Elburz Mts., near Asadbar, and near Ahar by Bornmüller (Bull. Herb. Boiss. ser. 2, 7: 434–435. 1907).

7. (*C. pontica* C. A. Mey., Mem. Acad. Petersb. ser. 6, Sc. Nat. 7: 14. 1850.) Caudical leaves broadly oblanceolate, narrowly petiolate; cauline leaves ovate-lanceolate, amplexicaul, slightly auriculate; stem 5-branched from near base upward, branches remote, elongated, arcuate-strict; peduncles and involucre fuscous-tomentose; involucre 15 mm high, densely pubescent with short gland hairs and hirsute with fine glandless yellowish hairs; corolla 20–21 mm long; ligule 2.5 mm wide; teeth 0.25–0.5 mm long; corolla tube 5–7 mm long, pubescent with stalked navicular hairs 0.05–0.25 mm long arranged singly or in pairs; anther tube 6 \times 1.5 mm; appendages 0.8 mm long, oblong, truncate or obtuse; filaments 0.75 mm longer; style branches 3.75 mm long, 0.15 mm wide, attenuate, yellow; achenes (not fully mature) 15-ribbed, ribs rounded, smooth, perhaps somewhat stronger than in typical plants; pappus yellowish-white, 8–9 mm long, 4-seriate. This plant was identified as *C. grandiflora* Tausch by Ledebour. Nordmann (Lenin ex Herb. Ledeb.) Guria or Mingrelia (= E. Georgia), Transcaucasia.

Relationship

C. conyzaefolia is the most primitive of all the *Crepis* species which are known to have 8 chromosomes, and it has the widest geographic distribution of any of these species. Its relationship to other primitive 4-paired species is therefore of considerable interest. Morphologically, it is closer to *C. pontana* than to any other species; its chromosomes, except for the absence of a medianly constricted pair, are also fairly similar. But it has a much wider geographic distribution. This may be due to the fact that it grows on soils deficient in lime, whereas *C. pontana* is restricted to calcareous formations. This difference in soil preference, indicating it is more adaptable, may be only one reason why *C. conyzaefolia* is the more successful of the 2 species.

The chromosomes of *C. conyzaefolia* also resemble those of *C. hokkaidoensis* and *C. chrysantha*; but these have a praemorse rhizome and they differ notably in their achenes, as well as in other characters. They occur, along with their polyploid relative, *C. polytricha*, in N.E. Asia. On the basis of gross morphology *C. alpestris* also appears to be fairly close to *C. conyzaefolia*, and natural hybrids occur between the two. But the chromosomes of *C. alpestris* are much more like those of *C. blattarioides* and *C. hypochaeridea*. Considering the morphological and cytological differences between these species, it appears that the most primitive 8-chromosome *Crepis* species comprise several different phylogenetic lines; but morphological evidence and geographical distribution indicate that they all had a common origin.

26. *Crepis blattarioides* (L.) Vill.

Hist. Pl. Dauph. 136. 1789. (Pl. 5. Fig. 44.)

Perennial, 0.4–7 (mostly 2–5) dm high; root stout, woody, elongated into a slender woody taproot (which is often broken off in dried specimens), strongly fibrous, bearing a narrow simple or divided caudex; stems flexuous or erect, 2–4 mm in diameter, terete, striate or sulcate, pubescent with fine pale hairs or glabrous, 1-headed or cymosely 1–5-branched toward summit, the branches pedunculate; caudical leaves few, disappearing early, 5–17 cm long, 1–2.5 cm wide, oblanceolate, acute, denticulate or dentate, gradually attenuate into the winged petiole, \pm pubescent with fine pale glandless hairs; lower cauline leaves similar, middle and upper cauline leaves lanceolate, acute or acuminate, denticulate or dentate, sessile, amplexicaul, acutely auriculate; peduncles 3–12 cm long, rather stout, sulcate, tomentulose and sometimes thickened near the head; heads erect, rather large, many-flowered; involucre dark green, campanulate, 12–15 mm long and nearly as wide in fruiting heads; outer bracts 8–10, with several subtending, sometimes pale or nearly glabrous, nearly equal to the inner bracts, lanceolate, acute; inner bracts 10–12, lanceolate, acute or obtuse, ciliate at apex, densely hirsute with long green black or yellowish setiform glandless hairs borne on each bract in a middorsal line, glabrous on inner face, not changed at maturity; receptacle alveolate, shortly and finely ciliate; corolla 20–23 mm long; ligule 2.25–3 mm wide; teeth equal or very unequal, 0.5–1.5 mm long, strongly glandular; corolla tube 5–6 mm long, glabrous; anther tube $5 \times 1.5(2)$ mm dis.; appendages 0.5–0.6 mm long, oblong, truncate, free; filaments about 1 mm longer; style branches 2–2.25 mm long, attenuate, yellow; achenes tawny, 5.75–8 mm long, 0.7–1 mm wide, fusiform, equally attenuate to both ends or more strongly upward, with expanded pappus disk, constricted at the pale-calloused base, subterete or subcompressed, the marginal rarely definitely obcompressed and with 3 stronger ventral ribs, about 20-ribbed, the ribs fine, rounded, smooth; pappus pure white or dusky, 6–8 mm long, 2–3-seriate, the setae unequal in length and width, $30\text{--}65\mu$ wide at base, very persistent. Flowering June–Aug.; flowers golden. Chromosomes, $2n = 8$.

Hieracium pyrenaicum L., non Rochel, nec Jard., et *H. blattarioides* L., Sp. Pl. ed. 1, 804. 1753.

H. blattarioides L., Sp. Pl. ed. 2, 1129. 1763.

Crepis austriaca Jacq., Enum. Vindob. 270. 1762.

Crepis sibirica Gou., Illust. Bot. 60. 1773, non L.

Catonia sagittata Moench, Meth. 536. 1794.

Lepicaune multicaulis et *L. turbinata* Lap., Hist. Abr. Pl. Pyr. 480. 1813.

Soyeria blattarioides Monn., Ess. 76. 1829.

Hieraciodes pyrenaicum O. Kuntze, Gen. 1: 345. 1891.

E. Spain on the mountain terraces of Valencia and Aragon (*vide* Willkomm, 203) and in the Pyrenees; W. and S.E. France, Alpes Maritimes, Hautes Alpes; French

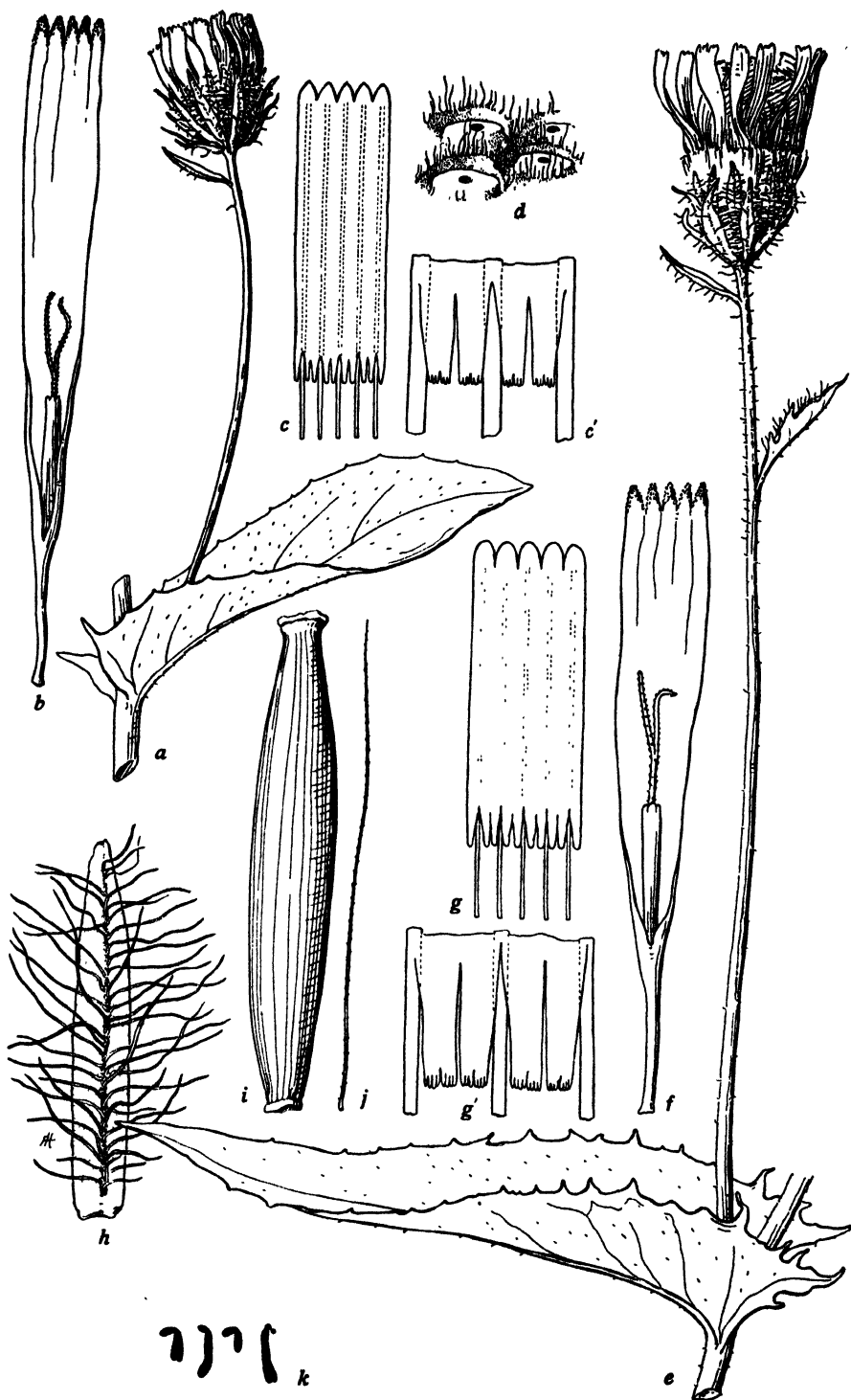


Fig. 44. *Crepis blattarioides*, a-d, from Jacquet in 1905 (UC 160355, cf. pl. 4, a); e-j, from Llena in 1901 (Bar, cf. pl. 4, b); k, from hort. genet. Calif. 2033 (seeds received from Roy. Bot. Gard. Edinburgh): a, head, peduncle, and cauline leaf, $\times 1$; b, floret lacking ovary, $\times 4$; c, anther tube, $\times 8$; c', detail of appendages, $\times 32$; d, detail of receptacle, $\times 25$; e, head, peduncle, and cauline leaf, $\times 1$; f, floret lacking ovary, $\times 4$; g, anther tube, $\times 8$; g', detail of appendages, $\times 32$; h, inner involucre bract, $\times 4$; i, j, achene and pappus seta, $\times 8$; k, somatic chromosomes, $n = 4$, $\times 1250$.

and Swiss Savoy and Jura; Alsace (Vosges) and S.W. Germany (Schwarzwald); Swiss Alps; German-Austrian-Italian Tirol; N.W. Balkan Pen. in Croatia (unverified). Although said by various authors to occur in the Carpathian Mts., it is not reported from that region by Pax. Montane and subalpine, from 700 to 2200 m alt.; frequenting forest borders among tall shrubs, especially on rich, rather moist, and often limy soil; forming dense clumps; sometimes in open places. In the middle E. Swiss Alps, acc. to Braun-Blanquet and Rübel (1487), it occurs only on rich limy soil and is frequent here and there in the Rhine area but does not occur to the east and south of this area.

The type of Linnaeus has not been seen by me, but in the general herbarium of the Muséum d'Histoire Naturelle in Paris I saw a specimen of *Hieracium pyrenaicum*, ex herb. Vaillant, which agrees with the two authentic specimens of Villars in the Grenoble Museum. A photograph of one of the latter is in the herbarium of the University of California (see pl. 5, a).

Observations of 19 different accessions under cultivation and of numerous herbarium specimens indicate that *C. blattarioides* is a rather variable species. Numerous minor forms have been given varietal names, but none of these, in my opinion, is of sufficient importance to necessitate recognition as a numbered variant, since they are all easily recognizable as this species (cf. de Candolle, 166, and note certain specimens cited below). One such form (var. *nana* Beauverd, ex Schinz et Keller, Krit. Fl. Schweiz, ed. 3, 360. 1914) is described as "4-8 cm high, with basal leaves during the flowering period, 1-headed, heads smaller than in the type." Although a striking form, this may have been merely the result of environmental conditions. See also $\times C. oenipontana$.

Spain: Catalanian Pyrennes, Valle de Aran, *Llenas* in 1901 (Bar); Catalanian Pyrennes, Aro, *Font Quer* in 1912 (Bar); Pyrennes, Republic d'Andorre, Arinsal, *Gandoger* in 1913 (Mo). **France:** central Pyrennes, Esquierry, *Grenier* in 1839 (K); Hautes-Pyrénées, Cauerets, le Pégùère, *d'Alleizette* in 1930 (UC); *ibid.*, valle d'Heas, *Sennen* in 1903 (UC); Hautes Alpes, Mt. Seuse, near Gap, *Faure* in 1936 (UC); *ibid.*, Lautaret, *Faure* in 1879 (K); Isère, without locality, *Villars* (Grenoble Museum) authentic; Isère, near Col de l'Alpe, *Lombard* in 1881 (Minn); Haute Savoie, Brison, *Bourgeau* in 1879 (K); *ibid.*, *Timothée* (DL), as var. *hirsuta* Ducomm. in herb. **Switzerland:** vallée de Nant, *Hall 12602* (UC); Canton Fribourg, Les Morteys, *Jacquet* in 1902, 1905 (Minn, UC); Vaud, Frénières, *Cornaz* in 1893 (Minn); Canton Valais, near Leuterbad, *Lomax* in 1885 (Minn); Lac Leman, Vevay, Taman, *Burnat* in 1848 (Bur); Valais, between Binneegg and Ausserlim, *Burnat* in 1898 (Bur); Alpes Lemaniennes, *Briquet* (DL) as var. *Lemaniana*, var. *Oddae*, and var. *genuina* Briquet in herb. **Italy:** Lombardy, Tirol, near Mt. Bilemone, *Porta* in 1883 (K, DL) as var. *rhaetica* Porta in herb.; Tirol, Mt. "Salzberg" near Hall, *Grembllich* (Bur, Minn); S. Tirol, above San Martino di Castrozza, *J. Ball* in 1877 (US). **Germany:** upper Bavaria, *Wolf* in 1895 (UC); *ibid.*, Aggenstein, *Zick* in 1901 (Bur). **Austria:** lower Austria, Mt. Schneeberg, "Saugraben" Valley (loc. class. *C. austriaca* Jacq.) *Döfler* (Bur, Minn); upper Austria, Vorderstoder-Loigesthal, *Niedereder* in 1902 (UC); *ibid.*, upper Styria, Mt. Schönfeldspitze, near Pusterwald, *Fest* in 1909 (Bur); *ibid.*, Sonnwendjoch, *Wojnar* in 1887 (US, Minn).

Relationship

Crepis blattarioides is very distinct from the other 3 species in this section, as well as from *C. alpestris*, with which it forms natural hybrids (cf. $\times C. oenipontana$). Although the chromosomes of these 2 species show very close resemblance in size and shape of each of the 4 pairs, yet the hybrids between them are completely sterile, indicating that the species are very different in genetic constitution. Apparently, the occurrence of these natural hybrids between *C. blattarioides* and *C. alpestris* is merely the result of a combination of favorable circumstances; but it certainly indicates some degree of relationship between sec. 8 and this one. On morphological grounds, however, *C. alpestris* is closer to *C. hypochaeridea* and other species of sec. 8 than to *C. blattarioides* and its closest relatives. Although *C. blat-*

tarioides is distinct in leaf shape and habit from *C. pontana* and *C. conyzaefolia*, yet its involucre, florets, and achenes are actually quite similar, especially to those of *C. conyzaefolia*. But, like *C. pontana*, *C. blattarioides* seems to prefer limy soils and it has a similar, more restricted distribution.

This edaphic restriction might seem to indicate that *C. blattarioides* is more primitive than *C. conyzaefolia*; and the larger cauline leaves and longer outer involucre bracts of *C. blattarioides* would support such an inference. But these morphological characters are offset by the more strongly ribbed achenes and the more primitive karyotype of *C. conyzaefolia*. Furthermore, two of the most primitive species in the genus, *C. sibirica* and *C. paludosa*, are widespread and evidently exist on a variety of soil formations, whereas the relic types like *C. pygmaea* and *C. terglouensis*, which have become adapted to alpine conditions, are restricted to calcareous formations. Therefore, wide edaphic adaptability is a more primitive feature than restricted edaphic tolerance in *Crepis*, and for this reason also *C. conyzaefolia* is a more primitive species than *C. blattarioides*.

SECTION 7. PALEYA

Relationships of the species

The 3 species of this section exhibit many resemblances, especially in the strong woody root, the woody caudex, which in *C. albida* and *C. elymaitica* exhibits a tendency to be suffruticulose, the numerous basal and few cauline leaves, few large or medium heads, numerous imbricate outer involucre bracts, which are of a different color or texture from the inner bracts, the inner bracts becoming carinate

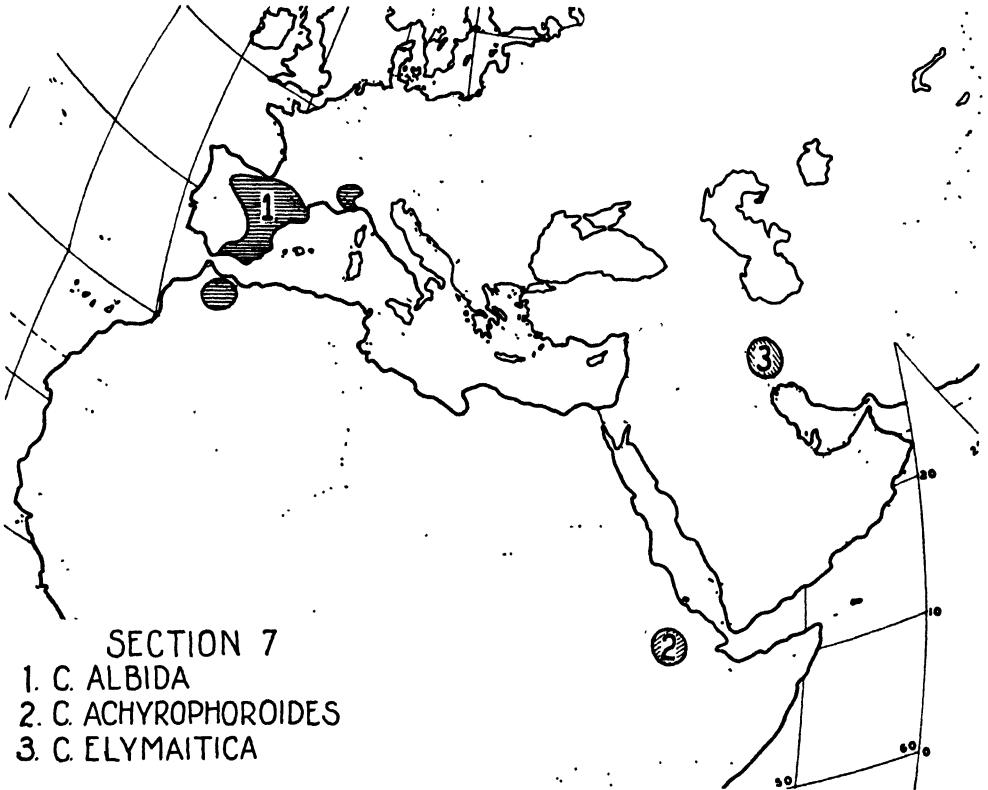


Fig. 45. Geographic distribution of the 3 species in sec. 7. Based on Goode Base Map No. 201 PC. By permission of the University of Chicago Press.

but otherwise little changed at maturity, and the achenes long and strongly attenuate or definitely beaked. Another feature which is very rare in *Crepis* but is found in both *C. albida* and *C. achyrophoroides* is the relatively long corolla tube, a condition characteristic of *Lactuca*. This is very marked in the latter species and is notable in 4 of the 6 subspecies of *C. albida*. *C. achyrophoroides* also possesses another feature which is characteristic of *Lactuca*, i.e., the peculiar cluster of hairs at the summit of the corolla tube. Furthermore, this species exhibits definite similarities to such more advanced species as *C. alpina* and *C. rubra* of sec. 21 and *C. vesicaria proleptica* of sec. 27. Because of its larger heads, broader bracts, and unbeaked achenes, *C. albida* is considered to be more primitive than *C. achyrophoroides*, whereas comparison of the same characters in *C. elymaitica* place it as more advanced.

The geographic distribution of the 3 species is significant, since *C. albida*, the most primitive species, is farthest from the assumed region of origin of the genus,

whereas *C. elymaitica*, the most advanced, is comparatively near that region; and *C. achyrophoroides*, the intermediate one, is endemic in Abyssinia, a secondary center of distribution (fig. 45). Hence, the distribution of the species in this section is also in conformity with Matthew's principle.

Key to the Species of Section 7

Plants 0.3–7 (mostly 1–4) dm high; corolla tube finely pubescent or glabrous, without a cluster of long hairs just below the opening of the ligule.

Heads large, many-flowered; florets 16–22 mm long; corolla tube pubescent; achenes 8–18 (mostly 10–16) mm long, gradually attenuate to the apex, 10–20 (mostly 15)-ribbed, ribs equal; pappus 4–11 (mostly 6–9) mm long, white or whitish... 27. *C. albida*, p. 307

Heads medium, about 30-flowered; florets about 14 mm long; corolla tube glabrous; achenes 8–10 mm long, attenuate into a short beak, 10–13-ribbed, ribs unequal; pappus 5 mm long, white..... 29. *C. elymaitica*, p. 323

Plants 5–12 dm high; corolla tube finely pubescent and with a cluster of long hairs just below the opening of the ligule; pappus 7 mm long, tawny..... 28. *C. achyrophoroides*, p. 320

27. *Crepis albida* Vill.

Prosp. Hist. Dauph. 37, t. xii, f. 1. 1779; Hist. Pl. Dauph. 3: 139. 1789; Willd., Sp. Pl. 3: 1596. 1804. (Figs. 46–51.)

Perennial, 0.3–7 dm high; root strong, woody, elongated; caudex wider, often branched at the summit, covered near base with brown or yellowish petioles of old leaves; stems 1–3, erect, fistulose, striate or sulcate, simple and 1-headed or 1–3-furcate with long branches; caudical leaves numerous, up to 15–28 cm long and 5–8 cm wide, oblanceolate, lanceolate or elliptical, attenuate into a winged petiole with broader base, base usually clasping and becoming coriaceous; cauline leaves few, sessile, lanceolate or linear; peduncles mostly long and stout, erect, not becoming larger near base of head; heads large, many-flowered; involucre cylindric, becoming campanulate in fruit, ultimately reflexed, at least in some forms; outer bracts 10–20, in 2 or 3 ranks, imbricate, the longest ultimately $\frac{1}{2}$ – $\frac{2}{3}$ ($\frac{3}{4}$) as long as inner bracts; inner bracts 12–28, in 2 ranks, like outer bracts with scarious often conspicuous margins, \pm canescent-tomentose or hispidulous with short yellowish gland hairs or glabrate, pubescent on inner face toward tip with whitish or yellowish silky appressed hairs, strongly keeled and indurate at maturity; receptacle alveolate-fimbriate, alveolae 0.5–1 mm wide, fimbriae fringed with fine white cilia; corolla 16–22 mm long; ligule pale, usually sulfur yellow, sometimes lemon yellow, with short gland-tipped teeth; corolla tube sparsely pubescent with short stout acicular hairs; anther tube yellow, 3.5–6 mm long; style branches 1.5–4 mm long, yellow; achenes pale yellowish, tawny or brown, elongated, fusiform, subterete, \pm attenuate to the slightly swollen apex, narrowed at the yellow calloused hollow often oblique base, with about 15 fine rounded ribs; pappus 4–11 mm long, white or whitish, fine, soft, shining, usually prominently extruded in mature heads, persistent. Flowering May–Aug.

Alps of N.W. Italy and S.E. France, Maritime Alps, mountains of S. France, Pyrenees, throughout Spain, Balearic Is. (Costa, Fl. Cataluna: 152, 1864), and in the Grand Atlas and other mountains of N. Morocco.

This notoriously polymorphic species is so extremely variable that it is difficult to distinguish well-marked subspecies. Although the more divergent forms are so distinct that several have previously been named as species, yet they are all connected by intergrading forms. Thus far it has been possible to obtain only 2 of these divergent types in living condition. When more of them can be examined

cytologically and observed under uniform conditions of culture, a more dependable classification will be possible. For the present it is proposed to recognize as subspecies the following groups of forms on the basis of a general tendency in each group to exhibit a certain peculiar combination of characters. That these groups are probably subspecific in nature, however, is indicated by the numerous intergrading forms and the restricted distribution of most of the groups as compared with that of subsp. *typica*. Some of the striking leaf variations found in this species, like many differences in size of plant, are undoubtedly the results of environmental differences, and for this reason many such variations found among the extensive herbarium collections have been passed over without even recording them among the numbered variants listed below. On the other hand, some differences in size and habit and certain leaf shapes seem to be characteristic of the plants found in certain areas, and these have been found useful in the recognition of subspecies.

Frequenting rocks and stony soil on calcareous formations over a considerable range of altitude, this species is sometimes subjected to extreme ecological conditions which probably account for reduced forms and certain other variations. An apparent connection between coastal conditions and development of tomentum has been noted below (p. 315). That the taller and longer leaved forms of all the subspecies are mostly to be referred to ecological conditions, such as shade, moisture, and crowding, is practically certain. But typical specimens of subsp. *macrocephala*, one of the taller subspecies, have been collected by the writer on a steep, fully exposed, stony bank. That the characteristically taller subspecies are genetically distinct entities is equally certain.

Key to the Subspecies of Crepis albida

Plant 0.3–3(4) dm high; stems simple or 1(rarely 2–3)-furcate.

Leaves obviously petiolate, oblanceolate or lanceolate, \pm glandular-hispidulous, often tomentulose, sometimes floccose, rarely glabrous.

Outer involucre bracts ovate, ovate-lanceolate or lanceolate; inner bracts lanceolate, obtuse, acute or acuminate.

Anther tube 4–5 mm long; appendages 0.5 mm long; plant not suffrutescent (range of the species)..... 27, *a. typica*, p. 309

Anther tube (4)5–6 mm long; appendages 1 mm long; plant suffrutescent (N. Spain)..... 27, *b. asturica*, p. 311

Outer involucre bracts lanceolate; inner bracts lance-linear, acuminate or filamentous at apex..... 27, *c. Grosii*, p. 311

Leaves obscurely petiolate, elliptical, obovate or oblanceolate, usually tomentose on both sides, tomentum feltlike, neither hispid nor glandular, rarely glabrous..... 27, *d. scorzonoides*, p. 315

Plant (1.5)3.5–5.5(7) dm high; stems 1–3-furcate.

Involucre about 10 mm wide at middle; inner bracts about 15 mm long; achenes chestnut brown..... 27, *e. macrocephala*, p. 317

Involucre 12–18 mm wide at middle; inner bracts 16–22 mm long; achenes yellowish or tawny..... 27, *f. longicaulis*, p. 317

27. *a. Crepis albida typica* subsp. nov. Planta 0.3–4 dm alta non suffruticosa; caulis plerumque monocephalus; folia caudicalia petiolata hispidula; involucre cylindricum, squamis exterioribus 10–16 ovatis vel lanceolatis, interioribus 12–20 lanceolatus obtusis interdum acutis; corolla 18–20 mm longa; antherae 4–5 mm longae flavae, appendicibus 0.5 mm longibus; achaenia fulva 10–17 mm longa.

Plant 0.3–3(4) dm high; \pm tomentose or glandular-hispidulous or glabrate; stems



Fig. 46. *Crepis albida typica*, *a*, from authentic spec. of Villar, Hautes Alpes (Grenoble); *b-e*, from Bicknell in 1914, Alpes Maritimes, Fiori et Bég. exsic. 2595 (BML 23461); *f-h*, from Lacaita in 1882, Alpes Maritimes (BML 2921); *k*, from Maire in 1926, Atlas rifain (UC 429471); *l-n*, from Lacaita in 1882, Italy, Piedmont (BML 2920): *a*, plant, $\times ca. \frac{1}{2}$; *b*, plant, $\times ca. \frac{1}{2}$; *c*, floret lacking ovary, $\times 4$; *d*, anther tube, $\times 8$; *e*, detail of appendages, $\times 32$; *f-h*, 2 achenes and a pappus seta, $\times 8$; *k*, plant, $\times \frac{1}{2}$; *l-n*, 2 achenes and a pappus seta, $\times 8$.

simple, or 1-furcate and 2-headed or rarely with 1–3 lateral pedunculate branches; caudical leaves oblanceolate or lanceolate, obtuse or acute, denticulate, dentate, lobed or pinnately divided, petiole short or rarely long; cauline leaves lanceolate or linear, acute or acuminate, or bractlike; (10)14–16, ovate, ovate-lanceolate or lanceolate; inner bracts 12–20, lanceolate, obtuse, acute or rarely acuminate; corolla 18–20 mm long; ligule 2–3 mm wide; anther tube (4)5 × 1.5 mm dis.; appendages 0.5 mm long, oblong; filaments 0.75 mm longer; style branches 3 mm long, 0.15 mm wide; achenes 10–17 mm long, yellowish, tawny or light brown; pappus 4–10 mm long. Flowers pale yellow, usually sulfur yellow. See fig. 46.

Hypochaeris tarazacifolia Moench, Meth. Suppl., 224. 1802.

Picridium albidum DC., Fl. ed. 3, 4: 16. 1805.

Lepicaune albida Lap., Abr. Pyr., 481. 1813.

Barkhausia albida Cass., Dict. Sci. Nat. 26: 62. 1826–1834.

Paleya albida Cass., *op. cit.*, 39: 393. 1826–1834.

Hieraciodes albidum O. Kuntze, Gen. 1: 345. 1891.

Throughout the range of the species, except N. Spain, in lower montane and montane regions, mostly from 500–2000 m alt.; usually on calcareous formations and frequently in fissures of rocks.

The type, in Grenoble Museum, is cited below; a photograph of this specimen is in the University of California Herbarium.

Italy: Piedmont, above S. Lorenzo, near Valdieri, *Lacaita* in 1882 (BML); Piedmont, Bardonecchia, *J. Ball* in 1879 (G); Maritime Alps, Tenda, valley of the Casterino, *Bicknell* in 1914 (K, BML exsic. Fiori et Bég. 2595); Maritime Alps, between Ormea and Bossietta, *Burnat et al.* in 1912 (Bur-S) m.v. 1; Maritime Alps, E. Mt. Galero, *Lereche et Burnat* in 1880 (Bur-S) m.v. 2. **France:** Monaco, environs, *Brugère* in 1912 (Bur-S) m.v. 3; Basses Alpes, *Fugeret* 89 (CP); Hautes Alpes, *Villars* (Grenoble in Herb. Villars!) type; Hautes Alpes, Rabau, *Lachman* in 1894 (Grenoble); Gard, Cevennes, *Planchon* in 1854 (Ms); Hautes Alpes, Monétier-les-Bains, *Faure* in 1911 (UC); Lozère, Cosse Mejan, opposite Florac, *J. Gay* in 1821 (K); E. Pyrenees, Corbières, Mt. Alarie, *Flahault* in 1888 (Ms); Hautes Pyrenees, near Gèdre, *Bodère* in 1856 (K, B, G, Ms, ex Herb. F. Schultz no. 308). **Spain:** Catalonia, El Monsech, *Riofrio* in 1925 (Bar, UC); Catalonia, Bages, Calders, *Font Quer* in 1910 (Bar); Catalonia, Monserrat, Vallfogona de Rincorb, *Garriga* in 1917 (Bar); Catalonia, Tarragona, Montroig, *Font Quer* in 1926 (Bar); Soria, Sierra Ministra, Castella, *Font Quer* in 1921 (Bar); Navarra, Portillo de Hundreño, above Legarda, *Lacaita* 33/27 (UC) m.v. 8; Burgos, Pancorbo, Penascol calisol, *Font Quer* in 1914 (Bar) m.v. 4; Albacete, Cerro del Jaral, near Alcaraz, *Cuatrecasas* in 1923 (Bar); Murcia, Calar del Mundo, *Cuatrecasas* in 1923 (Bar, UC); Albacete and Jaen, Sierra de Alcaraz and Segura, Mt. Mugron, *Porto et Rigo* 558 (K, 1 of 3 plants in this collection may be subsp. *scorzoncroides*); Jaen, Sierra de Segura, *Bourgeau* 771 (K); Jaen, Sierra Magina, valley of El Peru, *Cuatrecasas* in 1925 (Bar, UC); Andalusia, near Benaocaz, Dornajod, *Font Quer* in 1925 (Bar) m.v. 5; Andalusia, near Grazalema, *Font Quer* in 1925 (Bar, UC) m.v. 6; Andalusia, near Benaocaz, 1000 m, *Font Quer* in 1925 (Bar, UC) m.v. 7; Granada, Sierra de Mijas, Prieta and Alfacar, *Huter*, *Porto et Rigo* 358 (K, B, PD, UC); Malaga, Sierra de la Nieve, *Bourgeau* 307 (K, P) m.v. 6. **Morocco:** Atlas rifain, Mt. Azrou, 1800–1900 m. *Maire* in 1926 (UC, Alger); Mt. Lexhab (El Ajmas), peak, 2050 m, *Font Quer* 741 (UC).

Minor Variants of *C. albida typica*

1. Leaves acute or acuminate and pinnately parted, with remote lateral lobes; heads smaller than usual. *Burnat et al.* in 1912 (Bur-S), between Ormea and Bossietta, Maritime Alps, Italy.

2. Leaves up to 22 cm long, less than 2 cm wide, blade narrow, elliptic, acute at both ends, attenuate into a slender petiole equal to blade, lacking tomentum. *Lereche et Burnat* in 1880 (Bur-S), Mt. Galero, E. Maritime Alps, Italy.

3. Leaves long, acute, conspicuously canescent-tomentose, yellowish at base. As the general tendency throughout the eastern part of the range is toward scanty tomentum, this plant stands out as a noteworthy variant. It also indicates that excessive development of tomentum may be an effect of close proximity to the sea, which is in general agreement with the distribution of the more tomentose forms of S. Spain. *Brugère* in 1912 (Bur-S), environs of Monaco.

4. Achenes 9–10 mm long, light brown, with darker summit, not strongly attenuate; pappus 6–7 mm long, dusky en masse. *Font Quer* in 1914 (Bar), Penascol calisol, Pancorbo, Burgos, Spain.

5. Leaves, stems, and involucre ± canescent-tomentose; leaves lanceolate, acute, pinnately lobed, long petioled. *Font Quer* in 1925 (Bar), Dornajod, near Benaocaz, 1000 m, Andalusia.

6. (*C. albida* var. *floccosa* Cass., in herb.) Canescent-tomentose or -floccose throughout; leaves lanceolate, acute or acuminate, bipinnately lobed, petiolate. *Font Quer* in 1925 (Bar, UC), fissures of calcareous rocks, 1000 m, near Grazalema, Andalusia; *Bourgeau 307* (K, P), Sierra de la Nieve, Malaga, Spain; *Llena* in 1910 (Bar), La Cenie, Tarragona, Catalonia, Spain.

7. Flower stems only 0.3–0.5 dm high; heads typical; root stocks robust. *Font Quer* in 1925 (Bar, UC), fissures of calcareous rocks, 1000 m, near Benaocaz, Andalusia.

8. Caudical leaves oblanceolate, obtuse, sinuate-denticulate, narrow petioled; cauline leaves unusually large, lanceolate, with broad lacinate base; leaves, stems, and involucre sparsely canescent-tomentulose. *Lacaita 33/27* (UC), in rough bushy ground, Portillo de Hundreño, above Legarda, Navarra, Spain.

27, *b. Crepis albida asturica* (Lacaita et Pau) Bab., Univ. Calif. Publ. Bot. 19: 399. 1941. Plant 1.5–3 dm high, glabrate or sparsely tomentose; stems 1–8 or more, simple or 1–3-furcate or with 1–3 shorter lateral branches, sulcate or striate; caudical leaves narrowly oblanceolate, obtuse or acute, denticulate, dentate, sinuately lobed or pinnately divided, with narrow acute lateral segments, petiole narrow above the broader base; cauline leaves lanceolate, linear or bractlike, acuminate; outer involucre bracts 12–16, ovate to lanceolate, the longest often $\frac{3}{4}$ as long as inner bracts; inner bracts 14–24, lanceolate, obtuse; corolla 16–18 mm long; ligule 2–3 mm wide; corolla tube about 5 mm long; anther tube (4)5–6 × 1.5 mm dis.; appendages 1 mm long, oblong, acute; filaments 0.5 mm longer; style branches 2.5 mm long, 0.15 mm wide; achenes yellowish, tawny or pale brown, 10–18 mm long; pappus 6–8 mm long. Flowering June–July; flowers sulfur yellow ex descr., but in cultivated specimens (hort. genet. Calif. 2088) grown from seeds sent by Lacaita, they are lemon yellow. Chromosomes, $2n = 10$. See fig. 47.

Crepis asturica Lacaita et Pau, ex Lacaita, Cav. Rer. Bot. Acta, 1: 7. 1928.

In E. and S. central Asturia, Spain, the Cantabrian Mountains, rocky fissures and cliffs, calcareous formations.

Spain: Asturia (Oviedo), E. Cantabrian Mts., between Onis and Carreña (abundant), *Lacaita 559/25* (BML) type; Llanes, *Stephenson* in 1926 (BML); Peñas de Europa Mts., Barranco del Rio Cares, *Lacaita 548/27* (UC); central Cantabrian Mts., Mt. Pico de Arvas, *Durieu 288* (DC, K, DS).

Although so similar to subsp. *typica* as to make the classification of herbarium specimens difficult, this subspecies is distinct, in that its anther tube appendages are twice the length of subsp. *typica* and narrow, acute; the anther tube also tends to be longer. From observations on cultivated plants the flowers are lemon yellow in subsp. *asturica*, a shade never reported in subsp. *typica*. Lacaita's observation that subsp. *asturica* is suffrutescent agrees with the herbarium specimens seen and the habit of the plant under cultivation, where it produces a dense mound of herbage on elevated rootstocks. Unfortunately, the behavior of subsp. *typica* under similar conditions is not known to the writer. For the present, at least, subsp. *asturica* may be recognized. After further study it may be reduced to the rank of minor variant.

27, *c. Crepis albida Grosii* (Pau) comb. nov. Plant (0.7)1.5–3(4) dm high, densely hispidulous and/or finely gland-pubescent or ± canescent-tomentose or glabrate; stems simple or 1–2-furcate; caudical leaves oblanceolate or lanceolate, pinnately divided or lobed, with narrow acute segments or sinuately lobed or dentate or denticulate, acute or obtuse, petiole short, narrowly winged; cauline leaves few, small, lance-linear or linear, acuminate or bractlike; outer involucre bracts 14–16, lanceolate or (m.v. 1) ovate-lanceolate; inner bracts 16–22, lanceolate, acuminate

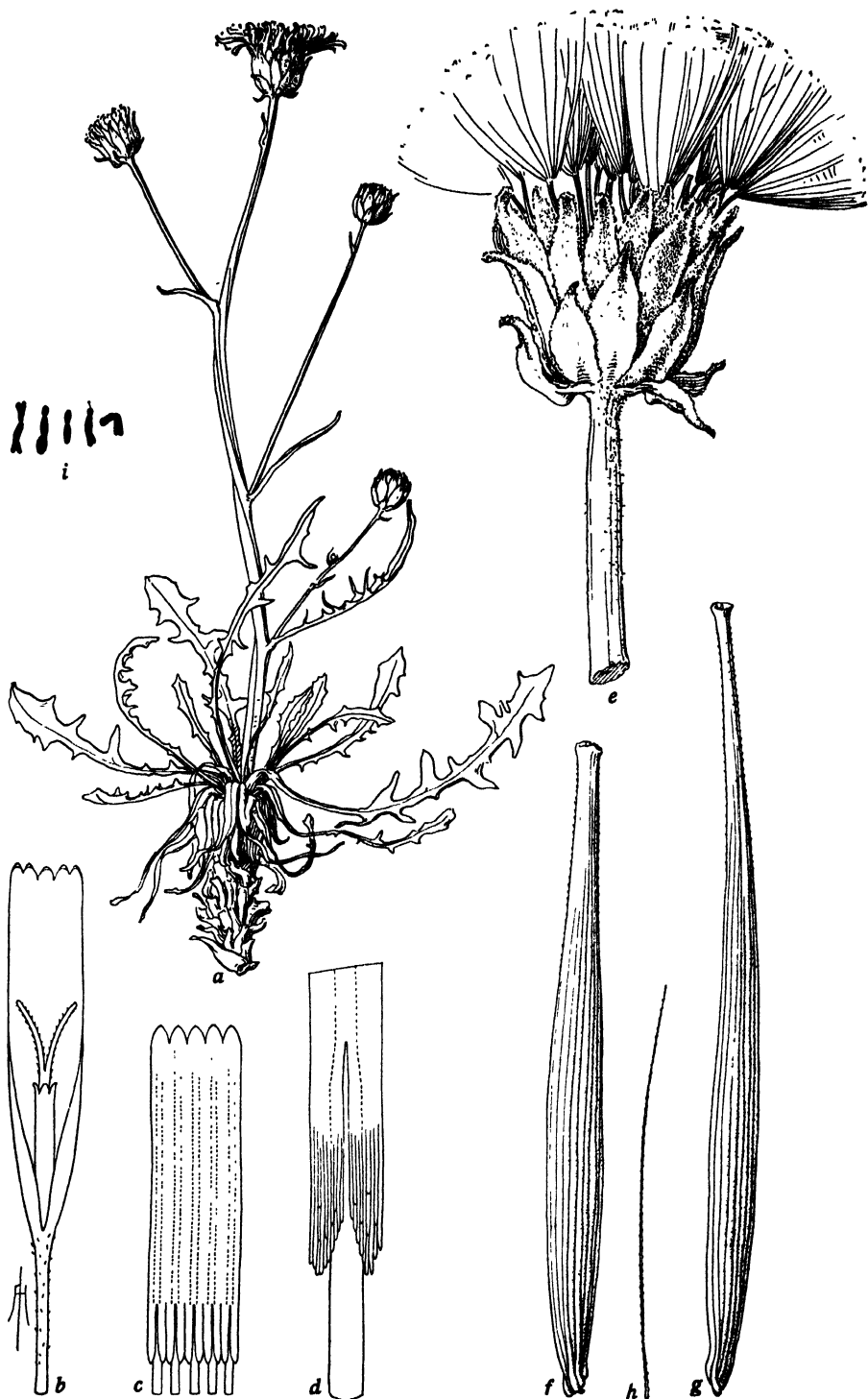


Fig. 47. *Crepis albida asturica*, a-d, from type (BML 28304); e-i, from hort. genet. Calif. 29.2088-4 (UC 669375): a, plant, $\times \frac{1}{2}$; b, floret lacking ovary, $\times 4$; c, anther tube, $\times 8$; d, detail of receptacle, $\times 32$; e, fruiting head, $\times 2$; f-h, 2 achenes and a pappus seta, $\times 8$; i, somatic chromosomes, $n = 5$, $\times 1250$.

or filamentous at apex; corolla 16–17 mm long; ligule 2–2.25 mm wide; corolla tube 5–6 mm long; anther tube (4)5 × 1 (1.25) mm dis.; appendages 0.5–0.75 mm long, united or free; filaments 0.5 mm longer; style branches 1.5–2.75 mm long, 0.1 mm wide; achenes deep yellow or light brown fading to pale yellow at summit, 9–16 mm long; pappus 6–9 mm long. Flowering May–July; flowers lemon yellow, according to Lacaita. See fig. 48.

Crepis Grosii Pau, Contrib. Fl. Granada, 23. 1916.

C. thrincifolia Pau, in herb.

S. Spain, mountains of Malaga, Granada, Jaen, and Almeria, on calcareous formations from 700–2400 m alt.

Spain: Malaga, Sierra Tejeda, Cartillo de Triglicena, *Gros* in 1915 (Bar) isotype and m.v. 9; Granada, El Maimon, around Velez Rubio, *Gros* in 1921 as *Crepis Grosii* Pau, in herb. det. Paul (Bar, UC) m.v. 10; Malaga, Sierra Tejeda, *Gros* in 1926 (Bar, UC) m.v. 11; Granada (?), Sierra Nevada, N. side, Domajo, *Lacaita 204/26* (BML) m.v. 12; Granada (?), "in rupibus montium Granat., 2300–7500 ft.," probably Sierra Nevada, *Boissier* in 1837 (K, B, Ms, SF, DS) collection includes very dwarf and tall forms, presumably from different altitudes, the former being densely hispidulous; Sierra Nevada, Horcajo de Frevelez, *Font Quer* in 1923 (Bar, UC) m.v. 13; Granada (?), Dientes de la Vieja, between Granada and El Molinillo, road to Diezma, *Lacaita 237/27* (UC) m.v. 16; Jaen, *Lacaita 295/25* (BML) m.v. 14; Jaen, Sierra de Jabalenz, near Jaen, *Lacaita 274/27* (UC) m.v. 14; Jaen, Aznatin, E. slope, *Cuatrecasas* in 1926 (Bar) m.v. 15; Jaen, Cortijo de los Prados, peñascos W. del serrate, *Cuatrecasas* in 1925 (Bar) m.v. 16; Jaen, El Boqueton, *Cuatrecasas* in 1925 (Bar) m.v. 17; Almeria, southwest of Velez-Rubio, *Ellman and Sandwith 536* (UC) m.v. 17.

Minor Variants of C. albida Grosii

This subspecies is well set off from all the others by a certain combination of characters, or rather of tendencies in certain characters. That it is highly variable, however, is evident from a comparison of the specimens identified as *C. Grosii* by Pau. Unfortunately, the type specimen is incomplete; and another plant of the type collection differs from all the other specimens identified by Pau as *C. Grosii* in several characters (cf. m.v. 9). Numerous other variants of this subspecies exist in the southern provinces of Spain (cf. m.v. 10–17). It should be noted here that the plant collected by Brandt (n. 2097 in Herb. Berol.) in the Sierra de Caratraca, Malaga, is not identical with any of the variants listed here and may not belong to this subspecies, although its short achenes (9.5–10.5 mm) and very short pappus (4.5 mm) may be merely extreme variations due to repression.

9. The specimen cited below is the only one in the type collection of this subspecies that has been seen by me. This plant differs from others identified as *C. Grosii* by Pau (see m.v. 10) in being densely glandular-hispidulous throughout, in the pinnately divided leaves (up to 2.5 cm wide), with narrow remote lobes, the somewhat narrower outer involueral bracts, and the short style branches (1.5 mm), narrow anther tube, and long narrow appendages (see fig. 48, a–f). Achenes lacking. No other plant closely resembling this isotype has been found among any of the collections referred to this subspecies. *Gros* in 1915 (Bar), Cartillo de Triglicena, Sierra Tejeda, Spain.

10. Canescent-tomentulose and sparsely glandular-pubescent; leaves sinuately or runcinately dentate or pinnately lobed; involueral bracts somewhat wider than in m.v. 9; style branches 2.75 mm long; anther tube wider; appendages 0.5 mm long, oblong, obliquely acute (see fig. 48, g–p). Achenes lacking. *Gros* in 1921 (Bar, UC), around Velez Rubio, El Maimon, Granada, Spain.

11. Low tomentulose plants; leaves runcinately or pinnately lobed; involucre as in m.v. 10. Achenes lacking. *Gros* in 1926 (Bar, UC), Sierra Tejeda, Granada (?), Spain.

12. Plants ± tomentulose, fairly robust, with several stems; involueral bracts mostly as narrow as in m.v. 9; achenes 9–13 mm long, yellowish-brown, with paler beak; pappus 8–9 mm long. *Lacaita 204/26* (BML), Domajo on calcareous rocks, 2000 m, Sierra Nevada, N. slope, Spain.

13. Leaves narrow (up to 16 mm wide), sinuately or runcinately dentate or lobed, minutely glandular-pubescent, with conspicuous straw-colored midribs and petioles; heads rather large; bracts more as in m.v. 10 and 11. *Font Quer* in 1923 (Bar, UC), Horcajo de Frevelez, 2400 m, Sierra Nevada, Spain.

14. Leaves, stems and involucre glabrous or glabrescent; heads somewhat larger and involueral bracts longer than in m.v. 9; leaves denticulate or sinuate-dentate or pinnately divided with narrow acute segments. *Lacaita 295/25* (BML) steep, calcareous rocks, Jaen, Spain; *Lacaita 274/27* (UC), on cliffs, Sierra de Jabalenz, Jaen, Spain.

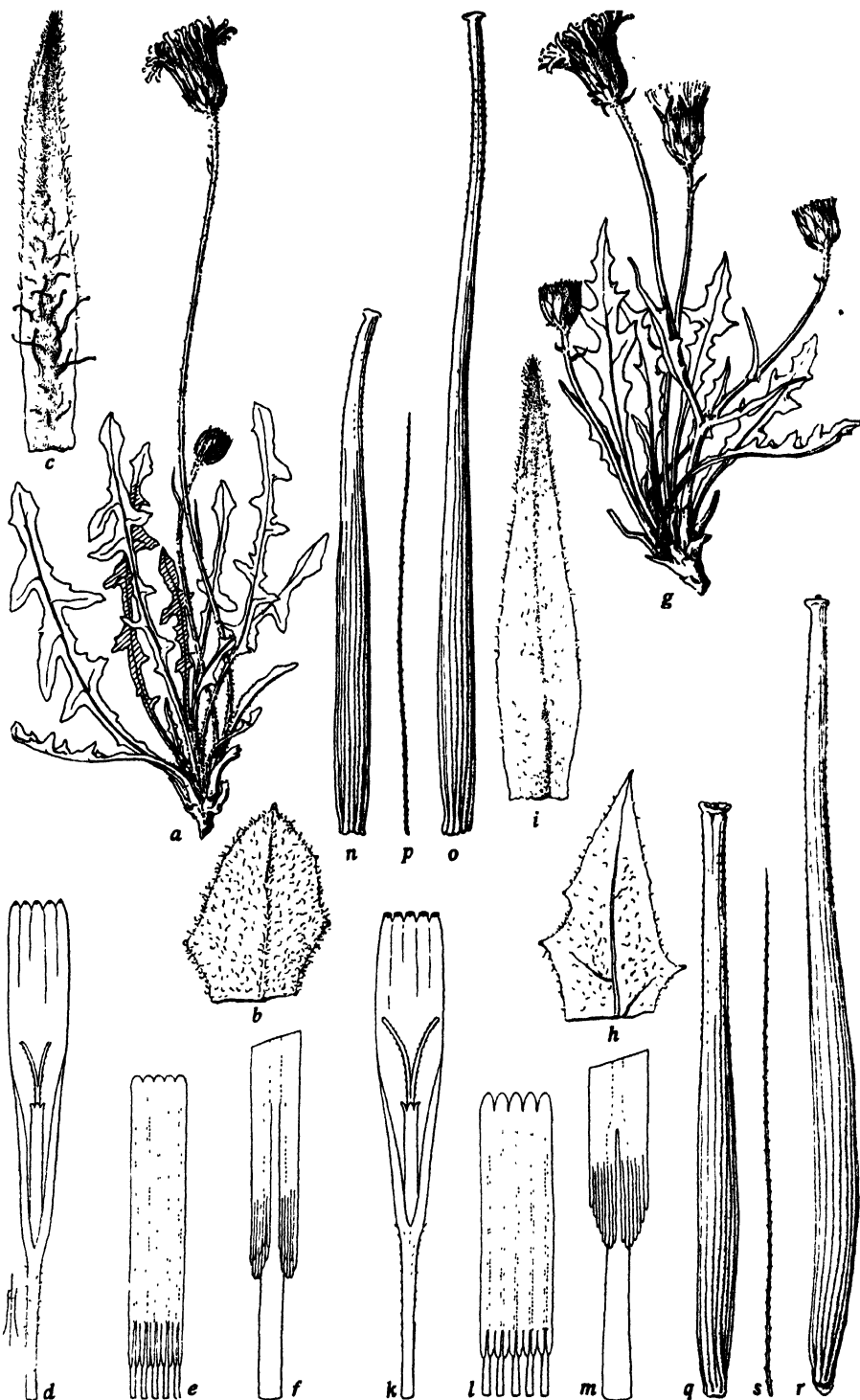


Fig. 48. *Crepis albida Grosii*, a-f, from isotype (Bar) m.v. 9; g-p, from Gros in 1921 (Bar, UC 446494) = *C. Grosii* Pau (det. Pau!); q-s, from *Lacaita 204/26* (BML, 29145) m.v. 12: a, plant, $\times \frac{1}{2}$; b, tip of leaf, $\times 2$; c, inner involucrel bract, $\times 4$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, plant, $\times \frac{1}{2}$; h, tip of leaf, $\times 2$; i, inner involucrel bract, $\times 4$; k, floret lacking ovary, $\times 4$; l, anther tube, $\times 8$; m, detail of appendages, $\times 32$; n-p, 2 achenes and a pappus seta, $\times 8$; q-s, 2 achenes and a pappus seta, $\times 8$.

15. Plants conspicuously canescent-tomentose, 0.7–2.2 dm high; leaves denticulate, dentate, runcinate or pinnately lobed. The feltlike tomentum is suggestive of subsp. *scorzoneroides*, but in all other characters the plants are subsp. *Grosii*. *Cuatrecasas* in 1926 (Bar), Aznatin, E. slope, 1710 m; *Cuatrecasas* in 1926 (Bar), Aznatin, W. slope, 1510 m; *Cuatrecasas* in 1926 (Bar), Puerto de la Vivora, 1600 m; *Cuatrecasas* in 1925 (Bar), Collado de Valle, 1200 m; *Cuatrecasas* in 1925 (Bar), Cerro del Buitre, 1100 m, Jaen, Spain.

16. (*C. thrincifolia* Pau, in herb.) According to C. C. Lacaita, Pau in a letter states that he distinguished this variant from *C. Grosii* by its entire or less lacinate leaves and greener less puberulent involucrel bracts. These characters are both too variable throughout the species to be of diagnostic value. In the specimen cited below the involucrel bracts are almost as tomentose as in some specimens of m.v. 10. *Lacaita 237/27* (UC), Dientes de la Vieja, between Granada and El Molinillo, road to Diezma, Granada (†), Spain.

17. Heads small; involucre 7 mm wide; inner bracts 15 mm high; stems 16 cm high, slender; caudical leaves up to 15 cm long, 3 cm wide, denticulate to runcinately or pinnately lobed, like stems and involucrel bracts, sparsely canescent-tomentose or gland-pubescent. *Cuatrecasas* in 1925 (Bar), El Boqueton, 1300 m, Jaen, Spain; *Ellman and Sandwith 536* (UC), near Velez-Rubio, Almeria, Spain.

Although highly variable, this group of variants, considered as a whole, exhibits sufficient homogeneity to warrant, at least for the present, its treatment as a subspecies. Further field observations, combined with cytological study and cultural experiments, may result in subdivision of this group or a change in its status. In addition to the narrower involucrel bracts, the flower heads tend to be smaller and the florets and style branches shorter, and the flower color is said to be lemon yellow. This subspecies occupies a definite geographic area.

27, *d. Crepis albida scorzoneroides* (Rouy) comb. nov. Plant 1.2–3 (4, 4.5) dm high, canescent-tomentose throughout, conspicuously so on leaves, lower stem, and involucre, tomentum often feltlike, especially on petioles, lower stem, and involucre, very rarely nearly glabrous; stem robust, simple or 1–3-furcate, striate; caudical leaves numerous, obscurely petiolate, elliptic, obovate or oblanceolate, obtuse or acute, irregularly denticulate or dentate or coarsely dentate or runcinately lobed, usually tomentose on both sides, tomentum feltlike, neither hispid nor glandular; cauline leaves ovate, acute or acuminate, or lanceolate or linear and bractlike; outer involucrel bracts 14–20, ovate or ovate-lanceolate, acute, apices free of tomentum and black or dark green; inner bracts 12–24, lanceolate, acute; corolla about 20 mm long; ligule 3 mm wide; corolla tube 9 mm long; anther tube (4)6 × 1.3 (1.5) mm dis.; appendages 0.6 mm long, obtuse; filaments 0.75 mm longer; style branches 3–3.5 mm long, 0.15 mm wide; achenes yellowish or tawny, 10–15 mm long; pappus 6–9 mm long. Flowering May–July; flowers pale yellow, probably sulfur yellow. See fig. 49.

Crepis scorzoneroides Rouy, Bull. Soc. Bot. Fr. 35: 120. 1888.

Coastal mountains of Alicante, Spain, especially the Mongo reg., near Denia (type locality) and southward; also S. Teruel, about 70 km from the coast; and an atypical form from Sierra de la Nieve near Ronda, Malaga; calcareous formations 300–1300 m.

Spain: Alicante, Denia, limestone cliffs of the Mongo, *Ellman and Sandwith 1151* (UC) type locality; Mongo Mts., *Font Quer* in 1923 (Bar) m.v. 19; Bernia Mts., near Benissa, *Gros* (Bar, UC); Sierra de Aitana, between Alcoy and Altea, *Font Quer* (Bar); Valencia, Mt. Monduber, near Gandia, *Font Quer* (Bar, UC); Teruel (†), Aragon, Sarrion (†), *Pau* in 1925 (BML) m.v. 18; Ronda, Sierra de la Nieve, *Gros* in 1922 (Bar, UC) m.v. 20.

Minor Variants of C. albida scorzoneroides

Apparently there is some connection between coastal environment and extreme development of tomentum in *C. albida*. Practically all specimens of subsp. *scorzoneroides* come from near the coast and some of the sporadic appearances of conspicuous tomentum in other subspecies are

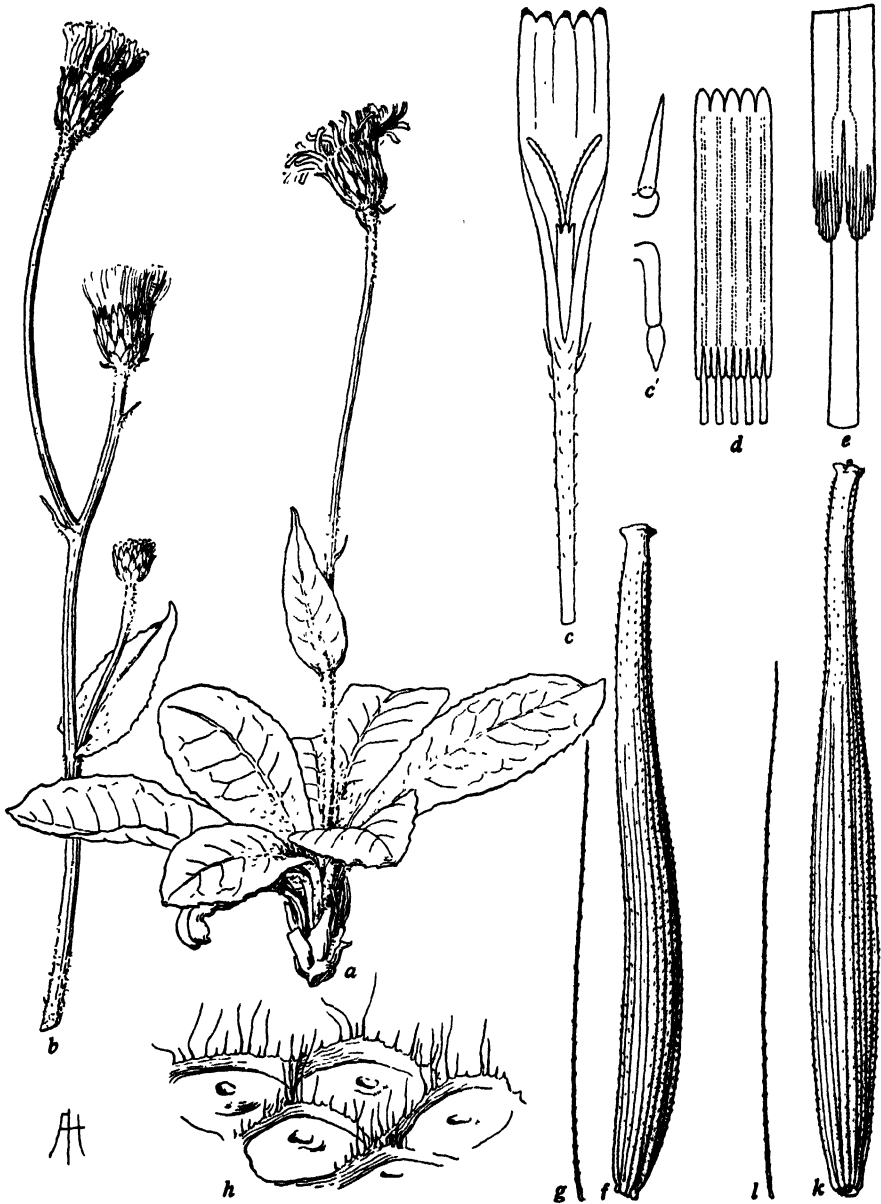


Fig. 49. *Crepis albida scorzoneroides*, a-g, from Gros, June 21, 1923 (UC 463919); h-l, from Font Quer, June 1, 1923 (UC 446511): a, plant, $\times \frac{1}{2}$; b, flower stalk, $\times \frac{1}{2}$; c, floret lacking ovary, $\times 4$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, g, achene and pappus seta, $\times 8$; h, detail of receptacle, $\times 25$; k, l, achene and pappus seta, $\times 8$.

from stations not over 40 km from the coast. At some of these stations, however, variants without much tomentum also occur, and a few plants with much tomentum have been seen from interior stations. Of special interest is Pau's almost glabrous plant (see below, m.v. 18) from the Aragon reg., which is about 70 km from the sea, although not separated from coastal conditions by any high mountains. But, aside from the apparent correlation between coastal conditions and the development of tomentum, there is an ensemble of characters peculiar to this subspecies which sets it off as a distinct entity. At the same time, its very close resemblance to subsp. *typica* in

many characters, and the existence of intergrading variants (cf. m.v. 19, 20, 22) are good reasons for its recognition as a subspecies.

18. Nearly glabrous; leaves sparsely tomentose on midrib and petiole; involueral bracts tomentose on margin. *Pau* in 1925 (BML), Ternel Prov. (†), Aragon reg., Spain.

19. Plant 4.5 dm high, very robust; stem 3-furcate; leaves coarsely and irregularly dentate or closely lobed, lobes acute, dentate. *Font Quer* in 1923 (Bar), Montgo, calcareous rocks, 300 m, in regno Valentini (= Mongo, between Denia and Javea, Alicante), Spain.

20. Leaves up to 23 cm long, oblanceolate, coarsely and irregularly dentate or runcinately lobed, segments acute or obtuse; heads smaller than usual. *Gros* in 1922 (Bar, UC), Sierra de la Nieve, Ronda, Spain.

27, *e. Crepis albida macrocephala* (Willk.) Babc., Univ. Calif. Publ. Bot. 19: 399. 1941. Plant (1.5) 2.5–7 dm high, robust, \pm tomentulose and/or hispidulous with or without glands, or glabrate; stems simple or 1–3-furcate, striate, fistulose; caudical leaves oblanceolate, acute or obtuse, denticulate, sinuately or runcinately dentate, or pinnately or bipinnately lobed, the lateral segments oblong, acute and dentate, petiole short or long, with a narrow wing above the broader base; cauline leaves lanceolate, sessile or nearly so, acute or acuminate, or bractlike; peduncles in furcate plants 5–25 cm long; heads not so large as in some forms of subsp. *scorzoneroides* or subsp. *longicaulis*; involucre cylindrical, up to 13 mm wide at middle; outer bracts 12–18, ovate; inner bracts 14–24, lanceolate, acute, or acuminate; corolla 18–22 mm long; ligule 2–3 mm wide; corolla tube about 8 mm long; anther tube (4.5) 6 \times 1.5 mm dis.; appendages 0.65–0.85 mm long, narrow, acute; filaments 0.5 mm longer; style branches 3.5–4 mm long, 0.15 mm wide; achenes chestnut brown, 8–12 mm long; pappus 9–11 mm long. Flowering May–Aug.; flowers sulfur yellow. Chromosomes, $2n = 10$. See fig. 50.

Barkhausia macrocephala Willk., Bot. Zeitung, 5(49): 860. 1847.

Crepis albida var. *major* Willk. et Lange, Prod. Fl. Hisp. 2: 248. 1870, part.

Barkhausia albida var. *macrocephala* Rouy, Fl. Fr. 9: 210. 1905.

Catalonia, Spain, coastal mountains and lower Pyrenees, calcareous formations, 700–1000 m alt.

Spain: Catalonia, Monserrat, *Font Quer* in 1917 (Bar) type locality; Monserrat, *Fremolo* in 1869 (Bar); Monserrat, Vallifogona de Rincorb, *Garriga* in 1918 (Bar); Catalonia, Igualada, *Font Quer* in 1926 (Bar); Catalonia (†), Castella Nova, Espinosa de los Monteros, *Font Quer* in 1926 (Bar); Catalonia, between Baños de S. Vicente and Sierra del Cadi, along trail from Arseguello to Ansobell, *Babcock* 391 (UC).

Besides being definitely characterized by its tall stature and its comparatively short, deep brown achenes, this group of variants occupies a definite geographic area. The less robust specimens and some of the leaf variations, however, exhibit intergradation with subsp. *typica*; and the whole ensemble certainly requires its inclusion here as a subspecies.

27, *f. Crepis albida longicaulis* subsp. nov. Planta robusta 2.5–5.7 dm alta glanduloso-hispida vel -hispidulosa et tenuiter tomentulosa; caules 1–2-furcati fistulosi; pedunculi (5) 10–28 cm longi; folia caudicalia interdum 23 cm longa 5 cm lata oblanceolata vel lanceolata; folia caulina lanceolata acuminata dentata vel pinnatifida; capitula magna; involucre cylindrica 20–25 mm longa 17–18 mm lata, squamis exterioribus 14–20 ovatis vel lanceolatis acutis, interioribus 14–28 lanceolatis acutis vel acuminatis; corolla circa 20 mm longa, ligula flavida circa 12 mm longa 2.5 mm lata, tubo pubescenti, pilis brevis crassis acicularibus; antherae 5–6 mm longae flavae; rami styli circa 4 mm longi flavi; achaenia fulva vel straminea 12–18 mm longa 10–20-costata; pappus albus vel flavidus copiosus persistens, setis inaequalibus 6–11 mm longis.

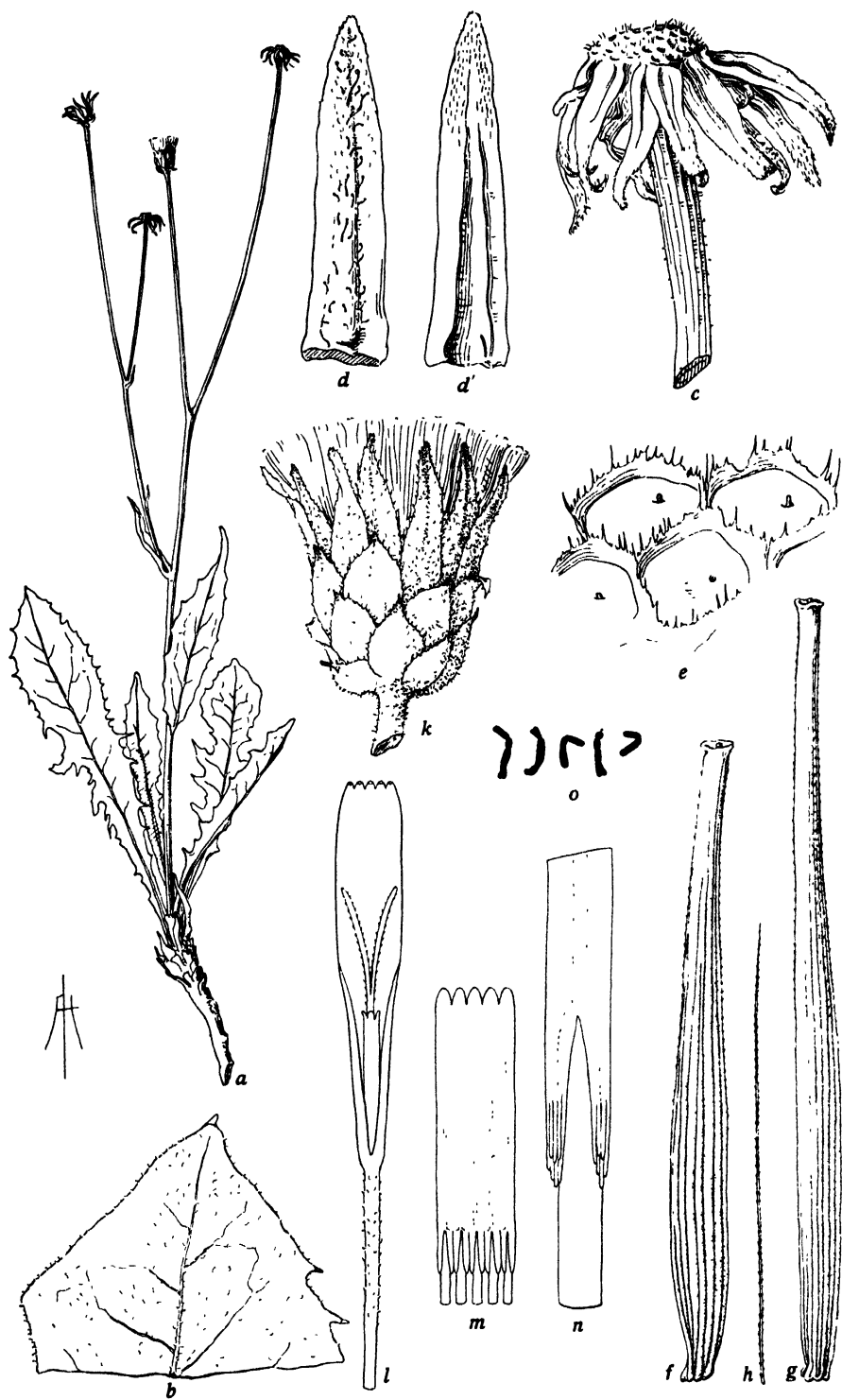


Fig. 50. *Crepis albida macrocephala*, a-h, from Babcock 391 (UC 429372); k-o, from hort. genet. Calif. 31.2957-8 (UC 669374): a, plant, $\times \frac{1}{4}$; b, tip of leaf, $\times 2$; c, old head, $\times 2$; d, d', inner involucral bract, outer and inner sides, $\times 4$; e, detail of receptacle, $\times 25$; f-h, 2 achenes and a pappus seta, $\times 8$; i, floret lacking ovary, $\times 4$; l, style lacking ovary, $\times 4$; m, anther tube, $\times 8$; n, detail of appendages, $\times 32$; o, somatic chromosomes, $n = 5$, $\times 1250$.

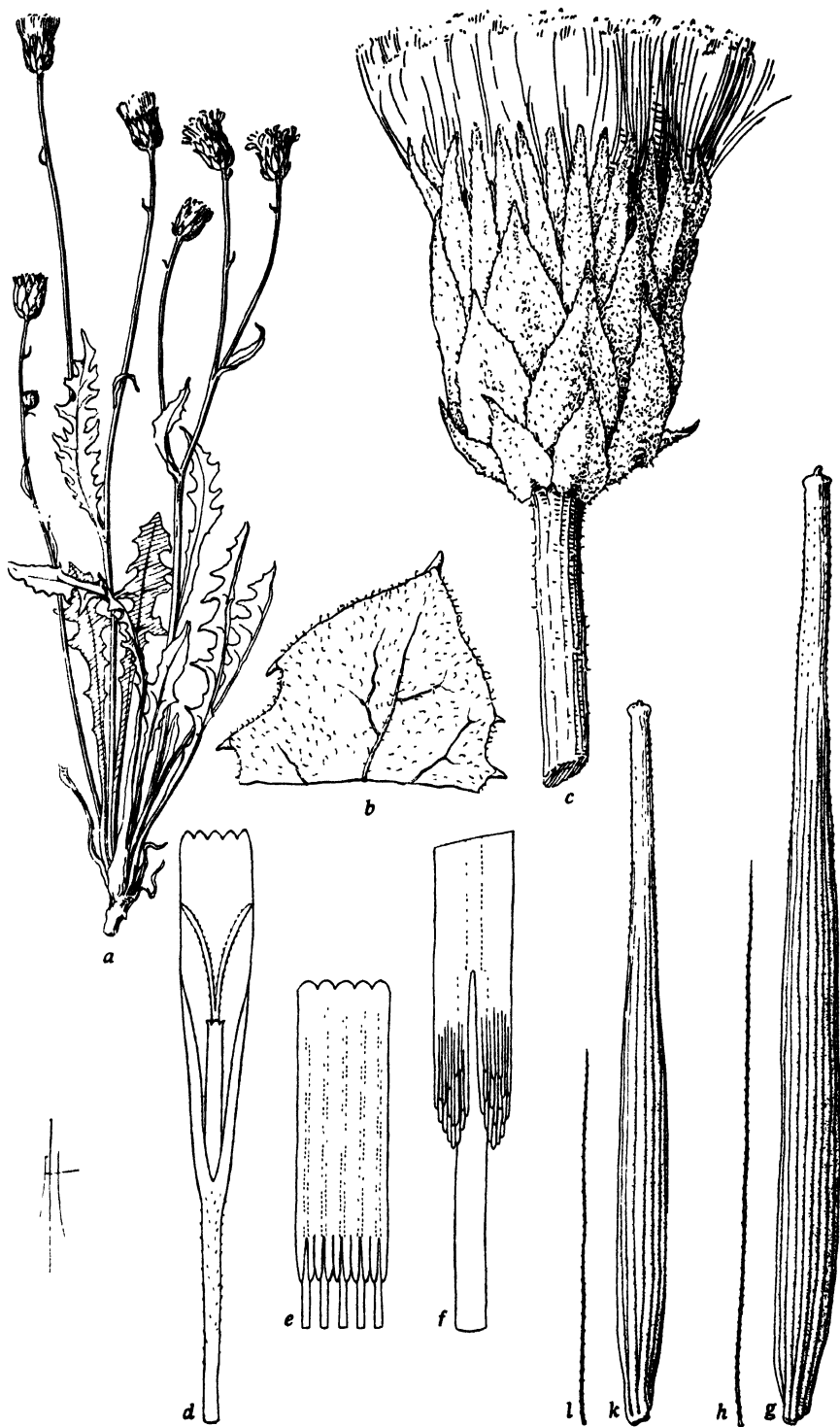


Fig. 51. *Crepis albida longicaulis*, from type (UC 346610): *a*, plant, $\times \frac{1}{4}$; *b*, tip of caudical leaf, $\times 2$; *c*, fruiting head, $\times 2$; *d*, floret lacking ovary, $\times 4$; *e*, anther tube, $\times 8$; *f*, detail of appendages, $\times 32$; *g*, *h*, *k*, *l*, 2 achenes, with pappus setae, $\times 8$.

Plant robust, 2.5–5.7 dm high, glandular-hispid or -hispidulous and sparsely tomentulose; stems 1–2-furcate, striate or sulcate, fistulose; peduncles (5) 10–28 cm long, with 1 or 2 small scarious bracts, not thickened at base of head; caudical leaves up to 23 cm long, 5 cm wide, oblanceolate or lanceolate, acute or obtuse, denticulate or irregularly runcinate-dentate or lobed, the segments triangular, acute and dentate, petiole long or short, alate; cauline leaves lanceolate, acuminate, denticulate, dentate or lobed; heads very large; involucre cylindrical, 20–25 mm long, 17–18 mm wide at middle; outer bracts 14–20, ovate or ovate-lanceolate, acute; inner bracts 14–28, lanceolate, acuminate or acute; corolla 20 mm long; ligule 2.5 mm wide; corolla tube 8 mm long, beset with short stout acicular hairs; anther tube (5) 6×1.7 mm dis.; appendages 0.75 mm long, oblong-acute; filaments 0.75 mm longer; style branches 4 mm long, 0.15 mm wide; achenes tawny with yellowish beak or straw colored, 12–18 mm long, 10–20 ribbed, ribs rounded and very finely spiculate, slightly swollen below pappus disk, the basal callus whitish; pappus 6–11 mm long in the same head, copius, white or tinged yellow, persistent. Flowering June; flowers sulfur yellow (†), but, according to Lacaita, “very pale lemon yellow, some almost whitish.” See fig. 51.

Central Spain, Segovia and Avila Provinces; and variants which intergrade with subsp. *scorzoneroides* in Alicante Prov. (see m.v. 22).

Spain: Avila, Pinar de Hoyocaserio (Avila, toward Sierra de Gredos), Lacaita 378/27 (UC) type locality; Segovia, Sierra de Guadarama, Cercidillo, gravelly soil in woods and in rocky fissures, montane, *Vicioso et Beltrau* in 1912 (Bar, UC); Alicante (†), Mt. Nariola, Gros in 1923 (Bar, UC) m.v. 21; Alicante, Bernia Mts. (near Benissa), Gros in 1923 (Bar) m.v. 22.

Although represented by very few collections, this subspecies is clearly set off from the others by its tall stature and very large heads, by the yellowish-green color of the herbage and the similarity of the achenes to those of subsp. *typica*.

Minor Variants of C. albida longicaulis

21. More tomentose than the type of the subspecies, as well as densely glandular-hispidulous, tomentum yellowish; leaves lanceolate, acute, runcinately dentate, teeth triangular, acute. Gros in 1923 (Bar, UC), Mt. Nariola, Alicante (†), Spain.

22. Leaves more as in subsp. *scorzoneroides*, broadly obovate, obtuse, dentate, teeth retrorse, acute; tomentulose only on midribs and lower part of stems, densely gland-hispidulous; achenes broader and less definitely beaked than in type of subspecies, straw-colored, rather strongly ribbed. Gros in 1923 (Bar), Bernia Mts. (near Benissa), Alicante, Spain.

Relationship

Crepis albida, in its tall forms, like subsp. *longicaulis*, shows more resemblance to *C. achyrophoroides* than to any other species, but the 2 species differ in many characters. In *C. albida* the heads are larger, the involucral bracts mostly broader, the florets larger, and the achenes are very gradually long-attenuate to the apex, instead of being definitely beaked, as in *C. achyrophoroides* and *C. elymaitica*. Thus, *C. albida* is the most primitive of the 3 species morphologically; but it is not closely related to any of the more primitive species in the genus.

28. *Crepis achyrophoroides* Vatke

Linnaea, 5: 514. 1875. (Pl. 6. Figs. 52, 53.)

Perennial, 5–12 dm high; root strong, vertical, woody, elongated; caudex 12–15 mm wide, brown-scaly, simple or 1-furcate; caudical leaves about 15 cm long, 4–5 cm wide, oblanceolate, obtuse or acute, runcinately or sinuately dentate and \pm denticulate, gradually attenuate into a very short winged petiole, pubescent on

both sides with short yellow glandless setules; lower cauline leaves oblong, acute or lanceolate, acuminate, sessile, rounded-auriculate, amplexicaul, dentate or denticulate, pubescent, middle and upper ones linear, acuminate, or bractlike; stem erect, rather stout, pubescent below, sparsely setulose above, simple and branched only near summit, the branches pedunculate or strongly branched from near base

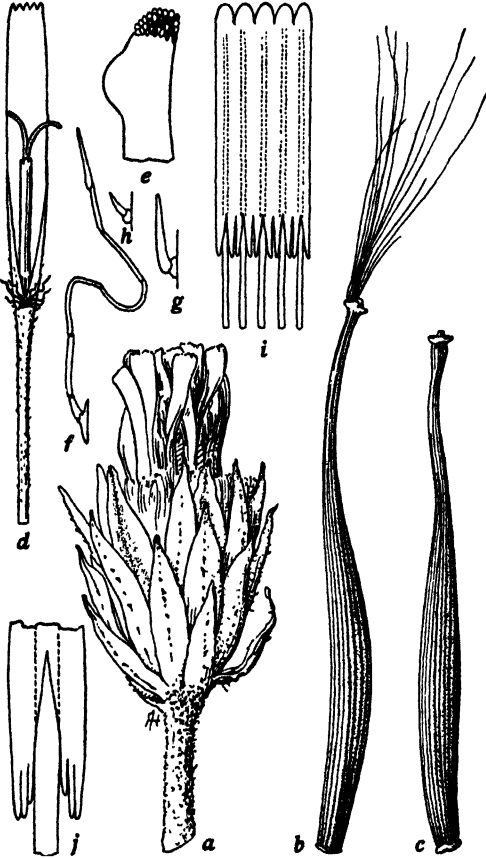


Fig. 52. *Crepis achyrophoroides*, b, c, from type (UWG); a, d–j, from isotype (US 945569): a, head, after anthesis, and part of peduncle, $\times 2$; b, c, inner and marginal achenes, immature, $\times 8$; d, floret lacking ovary, $\times 4$; e, detail of ligule tooth, $\times 50$; f, long trichome from top of corolla tube, $\times 25$; g, h, short trichomes from corolla tube, $\times 50$; i, anther tube, $\times 8$; j, detail of appendages, $\times 32$.

upward, the branches long, strict, 2–3-headed; peduncles 6–12 cm long, 1–2-bracteate, bracts setulose, tomentulose above; heads erect, large, many-flowered; involucre campanulate, 15–16 mm high, 10 mm wide, imbricate in anthesis, becoming differentiated into outer and inner series in fruit; outer bracts about 18, the longest $\frac{2}{3}$ as long as the inner bracts, lanceolate, acute, yellow, with a single median dorsal row of short black setules, shortly pubescent, like inner bracts densely pubescent on inner face with yellow shining hairs; inner bracts about 18, lanceolate, obtuse, ciliate at apex, yellow, with narrow or broad greenish dorsal median stripe, setulose and gland-pubescent with brown glands, becoming rounded-carinate and indurate, not spongy-thickened; corolla 17 mm long; ligule 1.25 mm wide; teeth 0.25 mm long; corolla tube 7 mm long, pubescent with minute 2-celled acicular hairs and with a ventral cluster of several-celled tortuous hairs at summit; anther tube 4×1.5 mm dis.; appendages 0.7 mm long, lanceolate, acute, free; filaments 1.25 mm longer; style branches 1.5 mm long; achenes (not fully mature) 9–10 mm long, light brown, fusiform, gradually attenuate into a definite beak, beak 3–4 mm long, coarse, ribs extending to summit, pappus disk slightly expanded, narrowed to the pale-calloused base, about 20-ribbed, ribs narrow,

rounded, very finely spiculate; pappus 7 mm long, tawny, 2-seriate, copious, fine, soft, deciduous. Flowering Aug.–Oct.; flowers yellow.

Hieraciodes achyrophoroides O. Kuntze, Gen. 1: 345. 1891.

Crepis billotioides Sch. Bip. in herb.

N. Abyssinia, the region northeast of Lake Tana, near Eritrea.

A specimen, determined by Vatke, in the general herbarium at the University of Vienna, is accepted as the type. In addition to the specimens cited below, there are (acc. to R. E. Fries: 354) specimens at Berlin and Stockholm. Photographs of the type and the isotype cited below are in the University of California Herbarium.



Fig. 53. *Crepis achyrophoroides*, from Schimper 778 (PC): *a, a'*, plant, $\times \frac{1}{2}$; *b*, head, $\times 2$; *c, c'*, inner, and *d, d'*, outer involucre bracts, dorsal and ventral, $\times 4$; *e-g*, 2 achenes and a pappus seta, $\times 8$. (Cf. pl. 6.)

Abyssinia: Sanka Berr, 2121 m, *Schimper 1223*, Oct. 8, 1863 (UWG type, US, UCf); Tigre or Begemeder, *Schimper 1223* (K); without definite locality, *Schimper 778*, Sept. 17, 1853 (PC, UCf) m.v. 1.

Minor Variant of C. achyrophoroides

1. (*C. billotioides* Sch. Bip., in herb.) Caudex 8 mm wide, leafy; stem erect, rather stout, branched above middle, branches few, long, remote, pedunculate; peduncles 4–10 cm long, covered with short black setules, tomentulose and somewhat thickened near head in fruit, 1–2-bracteate, bracts setulose on margin; involucre 17 mm high, 10 mm wide; outer bracts about 18, acuminate, unequal, longest $\frac{1}{2}$ – $\frac{2}{3}$ as long as inner bracts, yellowish, with dorsal median band of short dark glandless setae, like inner bracts pubescent on both sides with short appressed yellowish hairs; inner bracts about 18, olive green toward the apex, with broad scarious margins, dorsally keeled, keel dark brown, black-setulose toward apex, shortly gland-pubescent on lower half, the glands brown, becoming strongly nerved on inner face; receptacle naked; flowers lacking; achenes (mature) 11–12 mm long, reddish-brown, fusiform, attenuate into a beak equal to body, 18–20-ribbed, 5 ribs somewhat stronger and more strongly calloused at base; pappus 8 mm long. Fruiting Sept. The foregoing notes, in which differences and additional data are italicized, show how closely this plant corresponds with the type of *C. achyrophoroides*, so far as the two can be compared—flowers of *C. billotioides* being absent. *Schimper 778*, Sept. 17, 1853 (PC, UCf, ex Herb. Sch. Bip.), without locality, Abyssinia. (Fig. 53.)

Relationship

Crepis achyrophoroides, in its very distinctive, imbricated, parchmentlike outer bracts of the involucre, as well as in habit, shows marked resemblance to *C. albida*, especially to the taller forms, subsp. *longicaulis* and subsp. *macrocephala*. In the peculiar involucre and long coarsely beaked achenes, it also resembles *C. elymaitica*. Because of its strong perennial root, long outer involucreal bracts, and the long corolla tube, with the peculiar cluster of long hairs at the apex of the tube, a feature which is characteristic of *Lactuca*, *C. achyrophoroides* must be considered a primitive species. On the other hand, its peculiar involucre and long-beaked achenes resemble those of *C. alpina* and *C. rubra* of sec. 20; and in habit, leaves, and achenes it also resembles *C. vesicaria proleptica* of sec. 25. Thus, *C. achyrophoroides* is an important connecting species, and it would be of special interest to compare its karyotype with those of the other species mentioned.

29. *Crepis elymaitica* Bornm.

Beih. Bot. Centralbl. 32(2): 416. 1914. (Fig. 54.)

Perennial, 0.4–1.8 dm high; caudex woody, 0.5–1.5 cm wide, in old plants elongated up to 4–5 cm long and then suffruticulose, 1–2-furcate, with 1 stem of the season's growth per caudex, bases of old stems sometimes persisting; caudical leaves numerous, 2–9 cm long, 0.6–3 cm wide, oblong to oblanceolate, obtuse, mucronate or apiculate, remotely repand-dentate or runcinate-dentate, gradually attenuate to the base or with very short winged petiole, sparsely gland-pubescent with crisp yellow hairs; lower cauline leaves similar or sessile, the others gradually reduced, lance-linear, acute; stem erect, in reduced specimens 1–2-headed, in others remotely 1–3-furcate, 2–5-headed, sparsely gland-pilose; peduncles 1.5–6 cm long, 1–3-bracteate, \pm gland pubescent near base of head; heads erect, medium, about 30-flowered (estimated); involucre cylindric-campanulate, 8–12 mm long, 3–7 mm wide at middle in fruiting heads, \pm densely glandular; outer bracts 10–12, unequal, longest $\frac{1}{2}$ – $\frac{2}{3}$ as long as the inner, lance-linear, acuminate; inner bracts 12–20, lanceolate, acuminate, glabrous on inner face, becoming slightly carinate dorsally and thickened near base in fruiting heads; corolla about 14 mm long; ligule about 2.5 mm wide; teeth 0.5–0.7 mm long; corolla tube about 4 mm long, glabrous; anther tube 5 \times 1.5 mm dis.; appendages 0.7 mm long, lanceolate, acute; filaments 0.8 mm longer; achenes stramineous, 8–10 mm long, about 0.6 mm wide, the body fusiform,



Fig. 54. *Crepis elymaitica*, from isotypes, Strauss in 1908 (Weimar): a, plant, $\times 1$; b, head, $\times 4$; c, inner involucre bract, dorsal side, $\times 4$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g-i, marginal and inner achenes and a pappus seta, $\times 8$; j, detail of ligule tooth, lateral view, $\times 32$; k, plant, $\times 1$.

strongly attenuate upward into a beak 1–2.5 mm long and about 0.2 mm wide, funnel-form below the slightly expanded pale pappus disk, narrowed to the pale-calloused hollow base, 10–13-ribbed, ribs unequal with about 5 stronger, rounded, smooth or muriculate toward apex under lens; pappus white, 5 mm long, 1-seriate, setae about equally fine, coarsest about 30μ (4 cells) wide at base, rather rigid but pliable, persistent. Flowering July–Aug.; flowers yellow.

W. Persia, in high mountains. No details are available concerning elevations and ecology; but one of the original collections, var. *alpina* Bornm., evidently grew either at a high elevation or in an exposed dry location.

The type (Bornm., *op. cit.*, t. XIX, f. 1a) and isotypes, as intimated by Bornmüller (*loc. cit.*), may be a shade-form.

Persia: Luristan Prov., Nehawend (Nihavand) dist., Mt. Kuh-i-Gerru, *Strauss* in 1908 (Weimar type, UWG isotypes); N. Arabistan Prov., Schuturun-kuh (Shuturan Kuh) Mts., *Strauss 152* (Weimar) as var. *alpina* Bornm. (*loc. cit.*).

Relationship

Crepis elymaitica resembles *C. albida asturica* in the suffruticulose caudex, and it is rather similar to *C. albida* in branching habit of the stem. But it resembles *C. achyrophoroides* in its involucre, even though *C. elymaitica* is somewhat smaller, the outer bracts are not so numerous, and there is a definitely thickened dorsal keel on the inner bracts (whether spongy in texture at maturity is not known) which is not present in *C. achyrophoroides*, whereas in *C. albida* the inner bracts are strongly keeled and indurate but not spongy-thickened. The achenes of *C. elymaitica* are much like those of *C. achyrophoroides*, but they are smaller and have fewer ribs. The leaves of this species differ in shape from both of the others, and the flowers are much smaller. Thus, *C. elymaitica* appears to belong in this section, but it is a somewhat more advanced species.

SECTION 8. ANISORHAMPHUS

Relationships of the species

The 26 species of this section are characterized by the woody perennial root and strong sometimes suffruticose caudex, the erect leafy or bracteate stem or stems bearing few or several heads, the heads large or medium and many-flowered, the involucre bearing black setules or short gland hairs, the longest outer bracts $\frac{1}{2}$ – $\frac{3}{4}$ as long as the inner, the inner bracts of most species little changed in fruiting heads, the achenes brown or brownish, with a long or short usually rather coarse beak or in a few species not beaked, and the pappus yellowish or very rarely white. The 6 species which have been examined cytologically have 4 pairs of asymmetrical chromosomes rather similar to those of *C. blattarioides* of sec. 6.

The species of this section fall into 2 fairly distinct subsections on the basis of leaf size, pubescence of the involucre, and ecological relations. Subsection A, **Amplifoliatae**, contains 10 species, the first 6 being the most primitive species in the section. All 10 are characterized by larger leaves in proportion to height of the plant, especially by the larger cauline leaves; they all have black setules on the involucre and most of them have few if any glands on the involucre. These species all occur in mountains of E. Africa, except *C. cameroonica* and *C. alpestris* (see fig. 55), and several are found at higher altitudes than any species of subsection B. The bearing of the distribution of *C. alpestris*, from central to S.E. Europe and Asia Minor, on the problem of origin and distribution of the whole genus is discussed in Part I, p. 86. Furthermore, these species are obviously adapted to more mesophytic conditions than those of subsection B. Some of them, for example *C. kilimandscharica* and *C. Schultzei*, are known to occur in forests, and most of the others may be chiefly forestal.

Subsection B, **Parvifoliatae**, contains 16 species which are characterized by smaller leaves in proportion to height of the plant, especially by the bractlike cauline leaves; and all but one have glandular hairs or setules on the involucre. Only the first species in the subsection approaches the most primitive species of subsection A; and the group as a whole exhibits a fairly continuous gradation downward in size of heads, florets, and achenes. Furthermore, there are 4 species in this subsection which have the inner involucreal bracts spongy-thickened dorsally, at least near the base, in fruiting heads; whereas only 1 species of subsection A has developed such specialization.

The species of this subsection are distributed from Cameroon, Belgian Congo, Uganda, and Tanganyika southward to the Cape of Good Hope, except *C. subscaposa*, the distribution of which in S.E. Asia is believed to be as significant as the exceptional distribution of *C. alpestris* (see figs. 55 and 56). Nine of these species are known to occur on the "short grasslands" and savannas which cover most of the great continental plateau. Interestingly enough, *C. Gossweileri*, reported from "woods" of Angola, is the only species in this subsection with glandless setules on the involucre, but it has the small basal leaves and naked stems characteristic of the subsection and it probably occurs mostly in forest meadows. *C. subscaposa* of S.E. Asia occurs on meadows, plains, and exposed places. *C. chirindica* and *C. simulans* are both known only from Mt. Chirinda, which is in the Masetter dist. of S. Rhodesia. This district has an altitude of about 1000 m, and it is highly probable that these 2 species are also grassland dwellers. The same is probably true of *C. congoensis*, which is known only from Elisabethville, Belgian Congo, at an altitude of 1450 m. The polymorphic and widely distributed *C. scaposa* occurs on short grasslands and sometimes in exposed places on higher

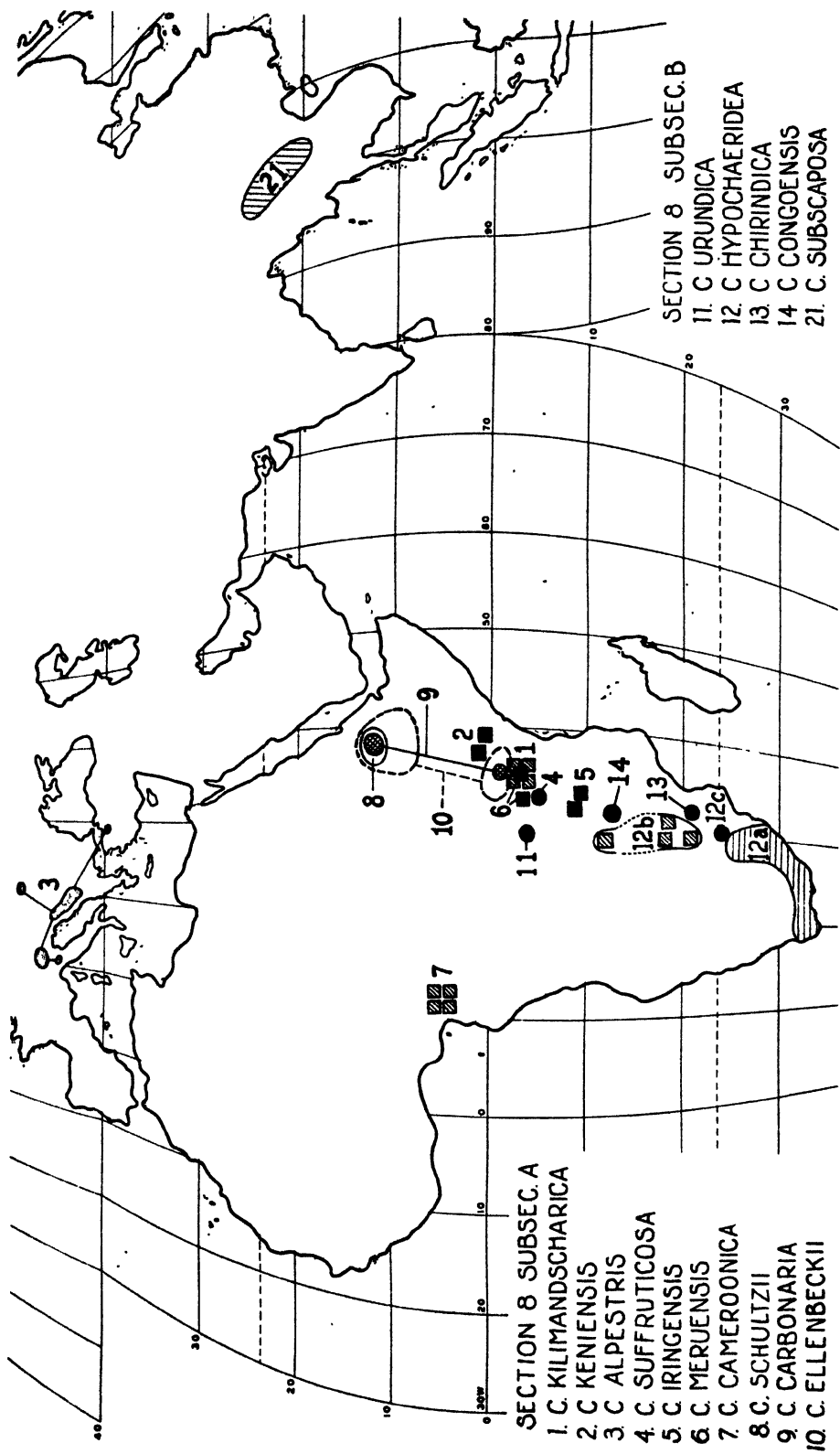


Fig. 55. Geographic distribution of the 10 species in sec. 8, subsection A, and 5 species of subsection B. Single stations are indicated by a solid circle, 2 known stations by solid squares, and 4 known stations by shaded squares. Based on Goode *Base Map No. 201 HC*. By permission of the University of Chicago Press.

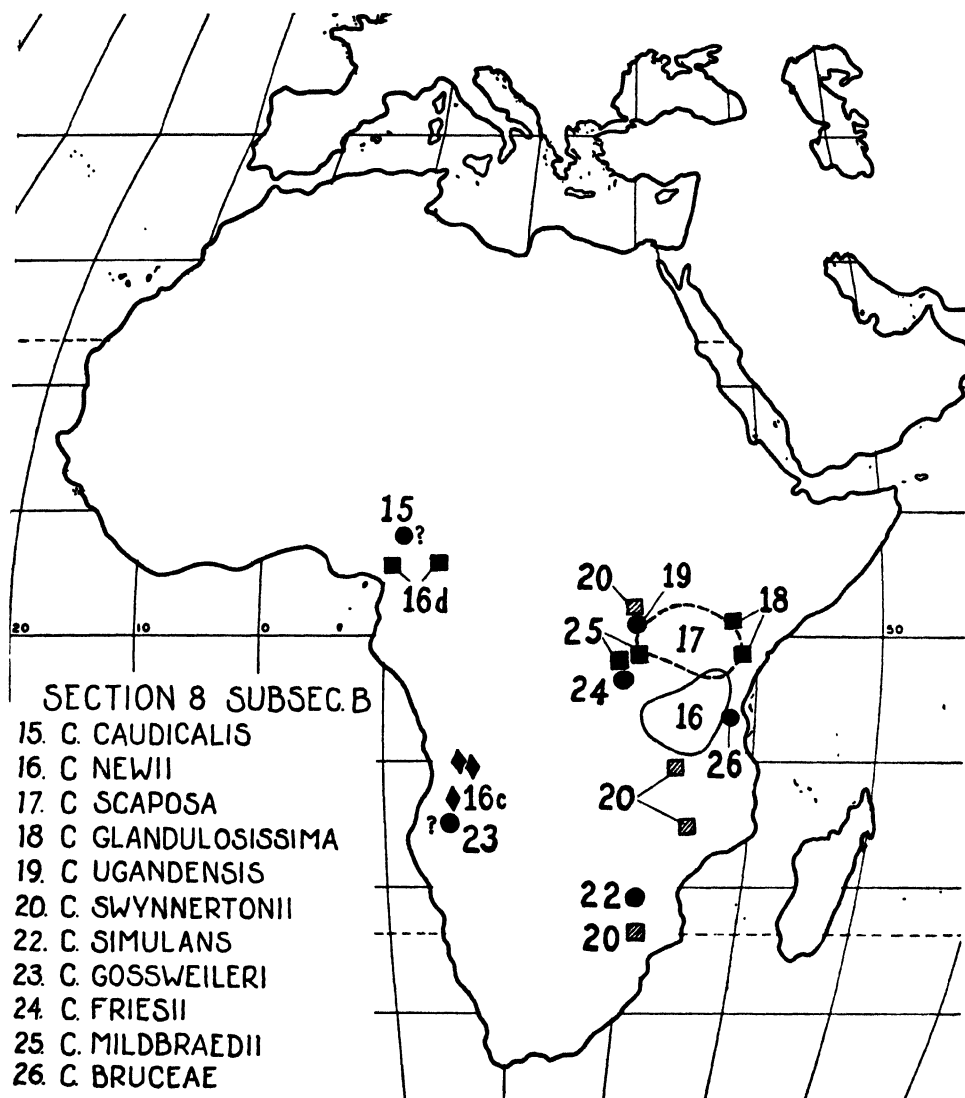


Fig. 56. Geographic distribution of the 11 other species in sec. 8, subsection B. Single stations are indicated by a solid circle, 2 known stations by solid squares, 3 stations by solid diamonds, and 4 stations by shaded squares. Based on Goode *Base Map No. 201 HC*. By permission of the University of Chicago Press.

mountains. Finally, only *C. urundica*, the most primitive species in this subsection, seems to be more definitely mesophytic in preference. It is known only from the type locality, described as a cool moist place at the base of hills 2050 m high. All the other species of this subsection are evidently more xerophytic than the species of subsection A; they are correspondingly more reduced in leaf size and for the most part in size of heads, florets, and achenes.

Taken as a whole, this section is certainly one of the more primitive in the genus. But, under the long continued favorable conditions provided in Africa, there has evolved a remarkable series of distinct species; and it is highly probable that with

further botanical explorations the number of species in this group will be considerably increased. A sufficient number are known, however, to warrant the conclusion that they were all derived from a Central Asiatic center and that, under increasing xerophytic conditions in Africa, the more primitive species have migrated into the higher mountains of the tropics in association with forests; and at the same time numerous more advanced species have come to occupy the grassy plains and exposed places of the central and southern part of the continent.

Key to the Subsections and Species of Section 8

- A Stems leafy, i.e., 2 or more of the cauline leaves relatively large and conspicuous or, if reduced (*C. Ellenbeckii*), the florets 7–9 mm long; involucre setose or setulose, the setae or setules black and in most species without glands. Subsection A. **AMPLIFOLIATAE**, p. 333
- B Plant suffruticose or suffruticulose; caudex either elongated with internodes 8–10 cm long or spreading with several branches forming a clump. *
- C Caudex elongated, bearing an elevated leafy rosette, caudical leaves narrowly lanceolate; lower cauline leaves broad at the base; corolla about 22 mm long; achenes strongly attenuate or beaked. Mt. Kilimanjaro 30. *C. kilimandscharica*, p. 333
- CC Caudex spreading, clump-forming; caudical leaves oblanceolate; cauline leaves narrow at the base; corolla 13 mm long; achenes gradually attenuate to the apex. Mt. Meru 33. *C. suffruticosa*, p. 339
- BB Plant not suffruticose or suffruticulose; caudex short, simple or 1–2 divided, not notably clump-forming.
- D Stem 9–15 dm high; cauline leaves, at least the lower one, oblanceolate. N. Abyssinia 37. *C. Schultzii*, p. 348
- DD Stem or stems 1–7 dm high; cauline leaves lanceolate or linear.
- E Florets well exerted in anthesis; corolla in marginal florets 15–23 mm long; achenes 6–10 mm long; pappus 5–8 mm long.
- F Stem or stems mostly 1-headed, sometimes 1–2-furcate, 2–3-headed, very rarely 4–5-headed; style branches 3 mm long. Europe; Asia Minor. 32. *C. alpestris*, p. 337
- FF Stem or stems more or less branched, several- or many-headed; style branches 1.5–2 mm long. Africa.
- G Inner involucre bracts glabrous on inner face; corolla in marginal florets 18–20 mm long; achenes merely attenuate or shortly beaked.
- H Involucres about 15 mm long; inner involucre bracts little if at all changed in fruiting heads; receptacle fimbriate, not ciliate.
- I Outer involucre bracts lanceolate, the longest $\frac{2}{3}$ as long as the inner; corolla tube pubescent, at least near base of ligule; anther appendages 1–1.3 mm long. Mt. Kenya. 31. *C. keniensis*, p. 335
- II Outer involucre bracts linear, the longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner; corolla tube glabrous; anther appendages 0.5 mm long. Mt. Meru; Mt. Kilimanjaro. . . 35. *C. meruensis*, p. 344
- HH Involucres 11–13 mm long; inner involucre bracts becoming definitely carinate and somewhat spongy-thickened in mature fruiting heads; receptacle finely ciliate. Iringa Prov., Tanganyika. 34. *C. iringensis*, p. 341
- GG Inner involucre bracts pubescent on inner face; corolla in marginal florets 15 mm long; achenes with a true beak equal to the body. Mt. Cameroon. 36. *C. cameroonica*, p. 346
- EE Florets scarcely or slightly exceeding the involucre in anthesis; corolla in marginal florets 5–11 mm long; achenes about 5 mm long (or possibly longer in *C. Ellenbeckii*); pappus 4–5 mm long.
- J Peduncles erect in anthesis, strongly nodding in fruit; heads larger; involucre 10–14 mm long, 5–7 mm wide at middle; corolla 5–6 mm long. N. Abyssinia and Mt. Kilimanjaro at 2800–3800 m alt. 38. *C. carbonaria*, p. 350
- JJ Peduncles always erect; heads smaller; involucre 8–10 mm long, 4–5 mm wide at middle; corolla 7–9(11) mm long. Abyssinia to Tanganyika at 1500–2600 m alt. 39. *C. Ellenbeckii*, p. 353

- AA** Stems bracteate, i.e., all the cauline leaves relatively small and mostly bractlike; involucre tomentose or pubescent with short gland hairs, or sometimes setulose and glandular, or if glabrous or setulose and not glandular (*C. scaposa*, *C. Gossweileri*), then the stems naked except for a few small bracts. Subsection B. **PARVIFOLIATAE**, p. 355
- K** Stem or stems scapiform, 1-headed, or 1-furcate and 2-headed.
- L** Leaves and stem glabrous, puberulous, or with a few short glandless hairs; involucre glabrous, sparsely pubescent or black-setulose; inner involucre bracts \pm appressed-pubescent on inner face with very fine hairs or glabrous. Kenya; Tanganyika; E. Belgian Congo. 46. *C. scaposa*, p. 376
- LL** Leaves and stem gland-pubescent; involucre densely glandular, with short yellow hairs and no black setules; inner involucre bracts strigulose, with yellowish shining hairs. Kenya Prov. 47. *C. glandulosissima*, p. 385
- KK** Stem or stems not scapiform, \pm branched, and several- or many-headed.
- M** Involucre 14–15 mm long, about 9 mm wide at middle; corolla in marginal florets 16 mm long, the ligule more than 2 mm wide; achenes not beaked. Belgian Congo. 40. *C. urundica*, p. 355
- MM** Involucre 6–13 (mostly 7–12) mm long, 3–8 (mostly 4–7) mm wide at middle; corolla in marginal florets 9–13 mm long, the ligule less than 2 mm wide; achenes beaked or, if not beaked, then the involucre only 6–10 mm long.
- N** Inner involucre bracts pubescent on inner face.
- O** Plant 5–9 dm high; caudical leaves up to 27 cm long, 2.7 cm wide; outer involucre bracts $\frac{1}{2}$ as long as the inner; heads about 35-flowered; style branches 2–3 mm long; achenes shortly beaked. Uganda. 48. *C. ugandensis*, p. 385
- OO** Plant 4–5 dm high; caudical leaves about 5 cm long, 1.4 cm wide; outer involucre bracts absent or displaced to summit of peduncle; heads about 17-flowered; style branches about 1 mm long; achenes not beaked. Belgian Congo, Ruanda reg. 53. *C. Friesii*, p. 396
- NN** Inner involucre bracts glabrous on inner face.
- P** Plant 6–8 dm high; caudical leaves up to 14–18 cm long.
- Q** Caudical leaves glabrous; involucre merely tomentulose, not setulose, 7–9 mm long, 3–4 mm wide at middle; heads about 20-flowered; achenes not beaked. N. Rhodesia; Belgian Congo. 49. *C. Swynnertonii*, p. 388
- QQ** Caudical leaves pubescent; involucre black-setulose, without glands, 11 mm long, 5 mm wide at middle; heads many-flowered; achenes with a beak equal to the body. Angola. 52. *C. Gossweileri*, p. 394
- PP** Plant 1–5 (or rarely 6) dm high; caudical leaves not over 11 mm long or, if sometimes 11–16 mm long (*C. Newii kundensis*), then found only in Cameroon and S.E. Nigeria.
- R** Plant suffruticulose; caudex spreading, clump-forming; caudical leaves 2–4 cm long, 1–1.5 cm wide; longest outer involucre bracts $\frac{1}{2}$ – $\frac{2}{3}$ as long as the inner; achenes light brown, 0.5 mm wide. Cameroon. 44. *C. caudicalis*, p. 367
- RR** Plant not suffruticulose; caudex short, simple or 1–2-divided, not notably clump-forming; caudical leaves mostly 5–11 cm long, 1.5–4 cm wide or, if sometimes less than 5 cm long, then the achenes 0.7–1 mm wide; longest outer involucre bracts $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner; achenes dark brown or reddish- or purplish-brown, 0.7–1 mm wide.

- S Inner involueral bracts becoming spongy-thickened, at least near the base, in mature fruiting heads; achenes not beaked or only shortly and coarsely beaked.
- T Caudical leaves glabrous, glabrescent or pubescent, but not glandular; ligules 1–2 mm wide; style branches 0.7–1.5 mm long; receptacle areolate, naked or shortly ciliate. Tropical Africa.....45. *C. Newii*, p. 369
- TT Caudical leaves gland-pubescent on both sides; ligules 1 mm wide; style branches 1.75 mm long; receptacle alveolate, the fimbriellae ciliate. S.E. Asia.....50. *C. subscaposa*, p. 391
- SS Inner involueral bracts little changed in fruiting heads, merely becoming indurate or sometimes \pm carinate, but not spongy-thickened; achenes definitely beaked except in the next.
- U Involucres 6–7 mm long, 4 mm wide in fruiting heads; achenes not beaked. Belgian Congo and Uganda.....54. *C. Mildbraedii*, p. 398
- UU Involucres 9–13 mm long, 3–8 mm wide in fruiting heads; achenes beaked or, if sometimes scarcely beaked (*C. hypochaeridea*), then the involucres 7–8 mm wide.
- V Largest leaves 3 cm wide; mature involucres 3–4 mm wide at middle; achenes 4 mm long, 0.3–0.4 mm wide. Tanganyika.....55. *C. Bruceae*, p. 401
- VV Largest leaves 1.5–2 cm wide; mature involucres 6–8 mm wide at middle; achenes 6–10 mm long, 0.6–1 mm wide.
- W Caudical leaves cuspidate, irregularly serrately dentate, glabrous on upper face; involucres fuscous-tomentose. Belgian Congo.....43. *C. congoensis*, p. 365
- WW Caudical leaves obtuse or acute, entire, denticulate or sinuately dentate, hispidulous or pubescent on both sides; involuere \pm canescent-tomentose.
- X Plant about 5 dm high; inner involueral bracts 16 in 2 unequal series; achenes 16-ribbed. S. Rhodesia, Mt. Chirinda....42. *C. chirindica*, p. 363
- XX Plant 1–3 dm high; inner involueral bracts 12–14, equal in length; achenes 10–13-ribbed.
- Y Involuere campanulate in fruiting heads, ultimately reflexed; outer bracts not purplish; corolla in marginal florets 10–11 mm long, the ligule 1 mm wide; style branches 0.5 mm long. S. Rhodesia, Mt. Chirinda.....51. *C. simulans*, p. 392
- YY Involuere broadly urn- or cup-shaped in fruiting heads, rarely reflexed; outer bracts purplish near the apex; corolla in marginal florets 11–13 mm long, the ligule 1.5 mm wide; style branches 1.2–1.5 mm long. Eastern half of S. Africa.....41. *C. hypochaeridea*, p. 357

SUBSECTION A. AMPLIFOLIATAE

30. *Crepis kilimandscharica* O. Hoffm.

Apud Engl., Pflanzenw. Ost-Afr. Nachbargeb., 422. 1895. (Fig. 57.)

Perennial, 6–13 dm high; caudex elongated, woody, annually recaulescent, internodes 8–10 cm long, 5–7 cm wide, leafy or covered with brown bases of old leaves; caudical leaves very numerous, up to 18 cm long, 3 cm wide, lanceolate, acute or acuminate, sinuate-denticulate or dentate, teeth apiculate, gradually attenuate into a broadly winged petiole, pubescent on both sides with short fine yellow glandless hairs, midvein dark, rather prominent; cauline leaves sessile, lanceolate, acuminate, lower ones with broad rounded subamplexicaul base, denticulate, pubescent, uppermost bractlike, setuliferous; stem erect, terete, fistulose, striate or sulcate, sparsely tomentulose and pubescent, remotely branched from near base or above middle, branches long, strict, few-headed, aggregate inflorescence cymose-corymbiform; peduncles 2–12 cm long, erect or arcuate, stout, bracteate, slightly thickened near head in fruit, fuscous-tomentose, pubescent with short fine black gland hairs and longer glandless setules; heads erect, large, many-flowered; involucre campanulate, 13–17 mm high, 5–7 mm wide near base in fruit, fuscous-tomentose, pubescent with unequal black glandless setules; outer bracts 10–16, unequal, longest $\frac{1}{2}$ as long as inner bracts, lance-linear, obtuse, ciliate at apex; inner bracts 12–20, lanceolate, obtuse, ciliate at apex, glabrous on inner face, in 2 series, inner ones much broader, membranous-margined, scarcely changed in fruiting heads; receptacle areolate-fimbriate, areoles 0.75 mm wide, fimbriae fleshy, with erect blunt protuberances bearing short fine yellowish deciduous cilia; corolla in marginal florets about 22 mm long; ligule 2.5 mm wide; ligule teeth 0.25–0.35 mm long; corolla tube 6 mm long, pubescent at summit with several-celled acicular hairs; anther tube 5.5×1.25 mm dis.; appendages 0.75 mm long, oblong, sagittate-acute; filaments very long, extending 1.75 mm beyond appendages; style branches 2.5 mm long, 0.2 mm wide, attenuate, yellow; achenes brown, 10–11 mm long, 0.75 mm wide, lightly compressed, lower half fusiform, constricted above the narrow oblique calloused base, 10–12-ribbed, ribs nearly equal, rather narrow, rounded, finely muriculate under lens, upper half gradually attenuate into the paler weakly ribbed beak, with strongly expanded pappus disk; pappus yellowish, 8–10 mm long, rather coarse, stiff, brittle, 3–4-seriate, not united at base, persistent. Flowering Aug.–Feb.; flowers yellow. Chromosomes, $2n = 8$.

E. Africa, Tanganyika Terr., Mt. Kilimanjaro; upper borders of the high forest from above Kiboscho to Useri, and on the Kifinika Volcano; southerly slope between the Umbwe and Wesu Wesu rivers, growing in moss on rocks in forest of *Philippia Johnstonii* and *Hagenia abyssinica*; altitudinal range, 2700–3500 m.

Monomorphic.

Kilimanjaro: above Kiboscho, 3000 m, and on Kifinika Volcano, *Folkens 1525* (B type, K, BB, UC); on the highest points of the upper connecting route above the Himo gorge, 2700 m, *Folkens 1845* (B, UC); south slope between Umbwe and Wesu Wesu rivers, 3100–3500 m, *Greenway 3161* (UC); Bismark Hill, 2800 m, *Greenway 3917* (UC).

Relationship

Crepis kilimandscharica has as its closest relatives *C. mruensis* of Mt. Meru and Mt. Kilimanjaro and *C. keniensis* of Mt. Kenya. It also shows affinity with *C. cameroonica* and, less strongly, with all the African species of *Crepis* occurring to the south of Tanganyika Terr., as well as some of the Abyssinian species, such as

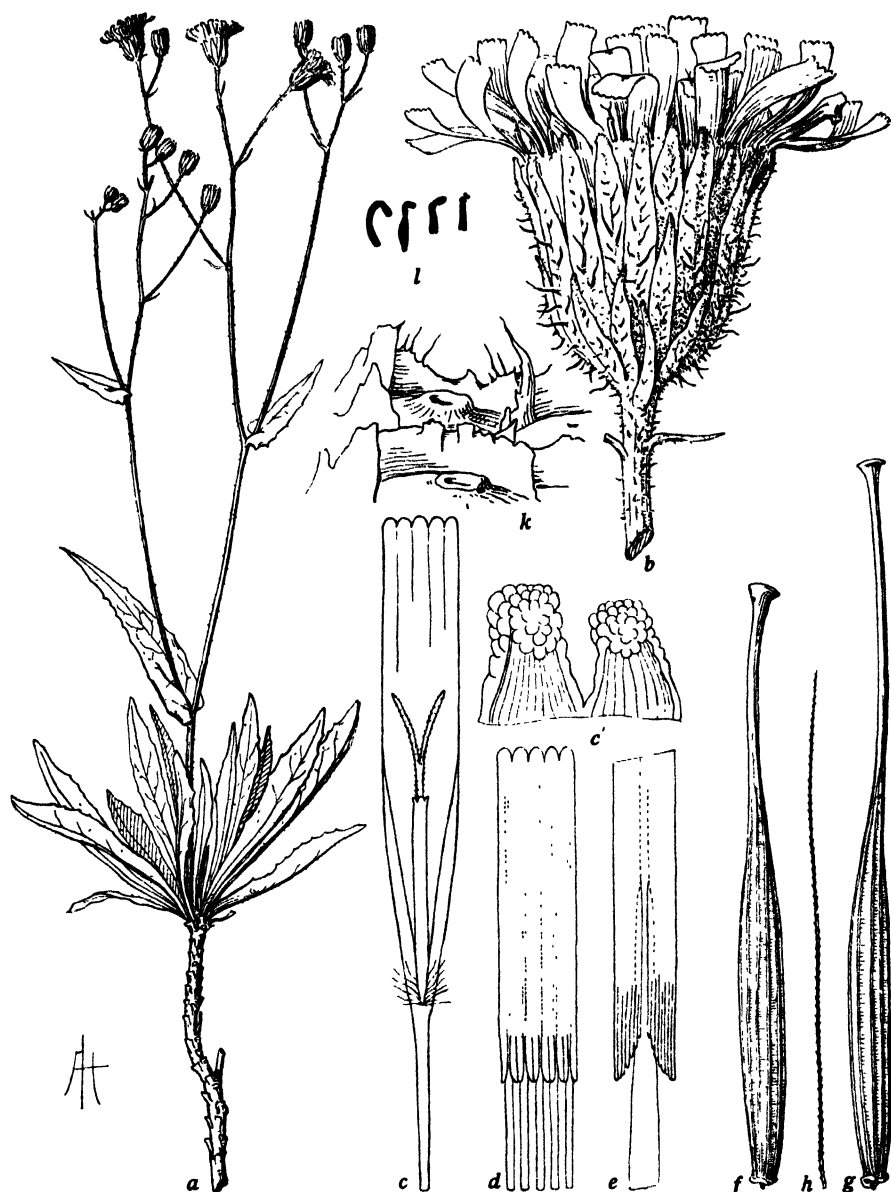


Fig. 57. *Crepis kilimandscharica*, a, f-h, from authentic spec., *Volckens 1345* (B); b-e, from isotype (K); k, from *Greenway 3917* (UC 519499); l, from hort. genet. Calif. 3280 (seeds received from Mt. Kilimanjaro, *Greenway 3745a*): a, plant, $\times \frac{1}{4}$; b, head, $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule teeth, $\times 50$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f-h, 2 achenes and a pappus seta, $\times 8$; k, detail of receptacle, $\times 25$; l, somatic chromosomes, $n = 4$, $\times 1250$.

C. Schultzii and *C. carbonaria*. But this species is unique in its annually elongated caudex, a primitive feature, and in the elevated rosette of caudical leaves of old plants. It is very distinct in many other respects.

31. *Crepis keniensis* (R. E. Fr.) comb. nov.

(Fig. 58.)

Perennial, 2.7–6.8 dm high; root vertical, slender, woody; caudex 1–2 cm long, 0.7–1 cm wide, simple or furcate, marked with old leaf scars below, leafy above; caudical leaves numerous, up to 33 cm long, 2.5 cm wide, oblanceolate, acute or acuminate, apiculate, sinuately or retrorsely dentate or denticulate, gradually attenuate into a long broadly winged petiole, with broader scarious base, pubescent on both sides with yellow glandless setiform hairs; cauline leaves similar or in small plants much reduced, middle and upper ones sessile, with narrow subamplexicaul base, uppermost bractlike, with black setules on lower face; stem erect, up to 0.5 cm wide and rather woody near base, fistulose above, terete, striate or sulcate, \pm pubescent like leaves, or glabrate below, remotely branched from below middle, branches long, arcuate, few-headed, aggregate inflorescence cymose-corymbiform; peduncles 1.5–12 cm long, stout, slightly thickened near head in fruit, bracteate, especially near head, flavescent-tomentulose, setuliferous like bracts and involucre, with unequal black glandless setules, sometimes with shorter yellowish gland hairs intermixed; heads erect, large, many-flowered; involucre cylindric-campanulate, 15 mm high, 5–7 mm wide near base in fruit, setulose, sometimes densely so, with black greenish and yellowish hairs intermixed; outer bracts 8–10, unequal, longest $\frac{2}{3}$ as long as inner ones, lanceolate, obtuse, ciliate at apex; inner bracts 12–16, in 2 ranks, nearly equal, inner ones broader, membranous-margined, lanceolate, obtuse, ciliate at apex, glabrous on inner face, scarcely changed in fruiting heads; receptacle areolate-fimbriate, areoles 0.5–0.75 mm wide, fimbriae fleshy, with rounded glabrous protuberances; corolla in marginal florets 20 mm long; ligule 2.5 mm wide; ligule teeth 0.2–0.4 mm long; corolla tube 7 mm long, irregularly beset near summit with a few stout acicular hairs 0.05–0.2 mm long, sometimes in clumps of 2 or 3; anther tube 4.5×1.2 mm dis.; appendages 1–1.25 mm long, oblong, obtuse; filaments 0.5–0.75 mm longer; style branches 1.75 mm long, 0.15 mm wide, attenuate, yellow; achenes yellowish-brown, 8–9 mm long, 0.75 mm wide, lightly compressed, fusiform, slightly constricted above the truncate calloused base, gradually attenuate above the middle into a very short coarse pale beak, with strongly expanded pappus disk, 10-ribbed, ribs narrow, rounded, finely muriculate under lens, some ribs extending to summit; pappus yellowish, 6–8 mm long, 2-seriate, rather coarse, stiff, elastic, not united at base, persistent. Flowering Jan.; flowers yellow.

Crepis kilimandscharica O. Hoffm. var. *keniensis* R. E. Fr., Svensk Bot. Tidskr. 22: 355–356. 1928.

E. Africa, Kenya Prov., Mt. Kenya, bamboo reg., 2350–3350 m.
Monomorphic.

Mt. Kenya: W. side, lower border of bamboo reg., near Forest Station, bank of a small stream, 2350 m, *Fries 678* (Upsala, UC) type; *ibid.*, upper bamboo reg., along stream, 2800 m, *Fries 1282* (Upsala); *ibid.*, 3325–3355 m, *Meinertshagen AH9409, 9408* (Amani, UC).

Relationship

Crepis keniensis is intermediate between *C. kilimandscharica* and *C. meruensis*, but is more like the latter in caudex and leaf shape; yet it is distinct from both of the others in shape of the achenes and floral features, especially in size of floret, anther tube, and appendages, and in the pubescence of the corolla tube. The 3

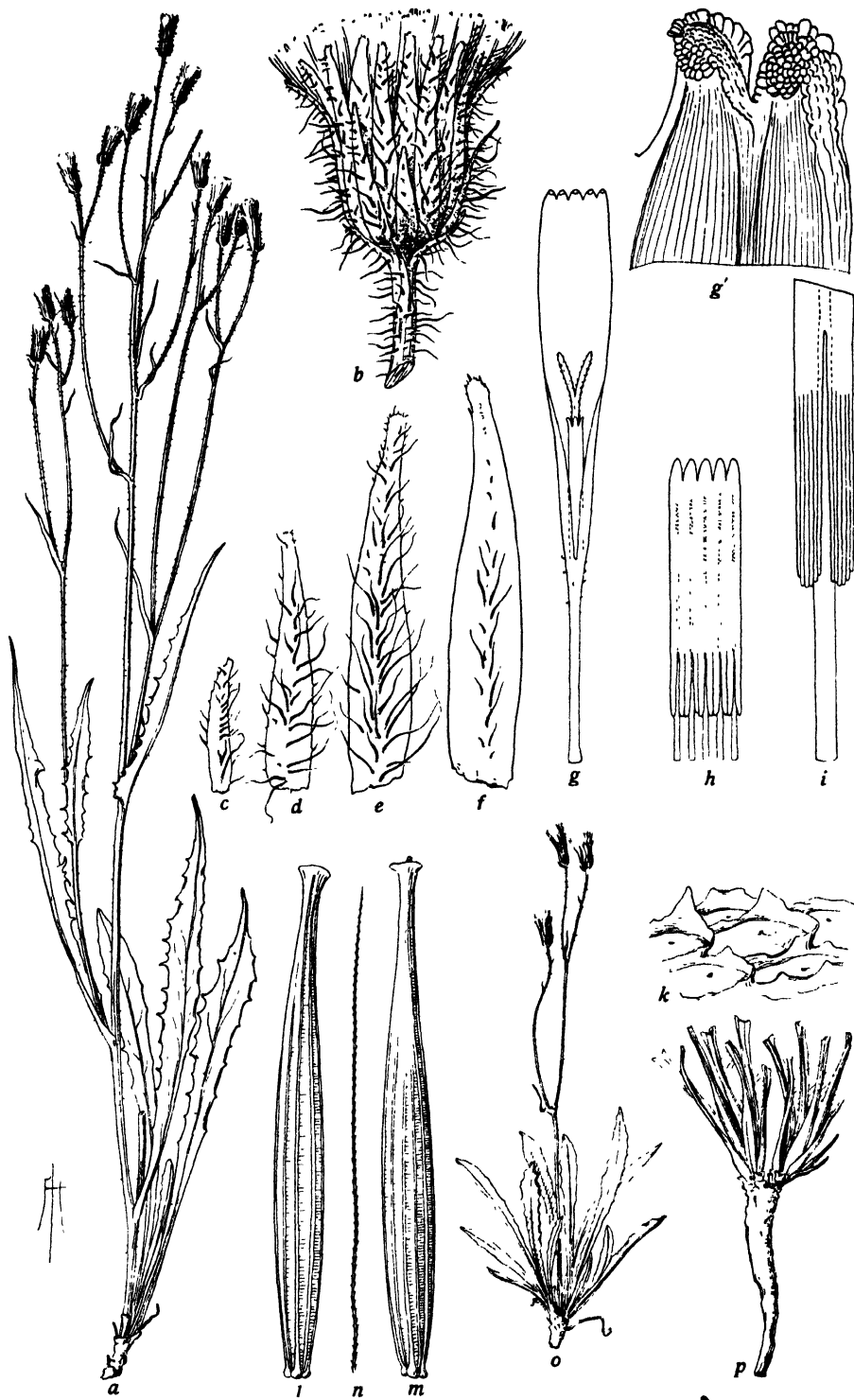


Fig. 58. *Crepis keniensis*, a-n, from type (Upsala); o, p, from Fries 1282 (Upsala): a, plant, $\times \frac{1}{4}$; b, head, $\times 2$; c-f, 2 outer and 2 inner involucral bracts, outer face, $\times 4$; g, floret lacking ovary, $\times 4$; g', detail of ligule teeth, $\times 50$; h, anther tube, $\times 8$; i, detail of appendages, $\times 32$; j, detail of receptacle, $\times 25$; l-n, 2 achenes and a pappus seta, $\times 8$; o, plant, $\times \frac{1}{4}$; p, base of plant, $\times \frac{1}{2}$.

species form a close assemblage, but they are certainly distinct species, and *C. kilimandscharica* is much more primitive in some characters than the other two.

32. *Crepis alpestris* (Jacq.) Tausch

Flora 11: 79. 1828. (Fig. 59.)

Perennial, 1–3.5 dm high; root stout, woody, often prolonged into a strong tap-root; caudex \pm swollen, simple or divided; caudical leaves persisting, 3–12 cm long, 0.7–2 cm wide, oblanceolate, obtuse or acute, denticulate to runcinate-pinnatifid or pinnately divided, with narrow lanceolate terminal segment and remote linear lateral lobes, attenuate into a winged petiole, pubescent with very fine short yellow glandular or glandless hairs, sparsely canescent-tomentulose, or glabrescent; cauline leaves 1–3(5), similar to caudical leaves or lanceolate, sessile, \pm amplexicaul; stem or stems erect, terete, striate or sulcate, canescent-tomentulose, simple and 1-headed or 2–3 (rarely 4 or 5)-branched, the branches pedunculate; peduncles elongated, stout, somewhat thickened and more densely tomentose near the head, often black-setulose with or without brown glands; heads erect, large, many-flowered; involucre campanulate, 9–16 (mostly 12–15) mm long, 7–12 mm wide at middle in fruit, dark green, grayish or yellowish tomentose, pubescent or setulose with black or green gland hairs; outer bracts 8–10, unequal, the longest $\frac{1}{3}$ – $\frac{2}{3}$ as long as the inner, lanceolate, acute; inner bracts 12–14, lanceolate, obtuse, ciliate at apex, \pm pubescent on inner face with appressed shining hairs, scarcely changed at maturity; receptacle areolate-fimbriate, areoles white, interspaces brownish, fimbriellae low, very shortly ciliate; corolla 17–23 mm long; ligule 1.75–2.25 mm wide; teeth 0.2–0.6 mm long; corolla tube 5–6 mm long, \pm pubescent with short (up to 0.3 mm long) coarse 2–3-celled acicular hairs; anther tube (4.25)5.25 \times about 1 mm dis.; appendages about 1 mm long, acute, united; filaments 1 mm longer; style branches 3 mm long, 0.1–0.2 mm wide, attenuate, yellow or very pale green; achenes pale brown, 7–10 mm long, subterete or somewhat compressed or obcompressed, strongly attenuate upward or coarsely beaked, sometimes paler and rarely sparsely ciliate near the summit, with slightly expanded pappus disk, constricted at the narrow pale-calloused base, 10–12-ribbed, ribs equal or somewhat unequal or sometimes 2–4 definitely stronger, finely muriculate; pappus yellowish-white, 5–8 mm long, 2–4-seriate, the setae unequal, 20–50 μ wide at base, pliable, very persistent, much exceeding the involucre. Flowering May–Aug.; flowers golden yellow. Chromosomes, $2n = 8$.

Hieracium alpestre Jacq., Fl. Austr. 2: 54, t. 191. 1774.

Crepis longifolia Hegetschw., Fl. Schweiz 766. 1839.

Brachyderea alpestris Sch. Bip. ex Nym., Consp. 455. 1865.

C. mucronata Ces. Pass. et Gib., Comp. Fl. Ital. 2: 457. 1878.

Hieraciodes alpestre O. Kuntze, Gen. 1: 345. 1891.

Switzerland, in the E. Alps, very rarely farther west; Germany, in the mountains of S.W. Bavaria; N. Italian Tirol and locally in the N. Apennines; mountains of W., Upper, and Lower Austria; W. Balkan states, south to Montenegro and Serbia; W. Carpathian Mts. in the Nieder Tatra Mts., acc. to Pax (228), who used this species as one of several indicators of calcareous soil; N.W. Asia Minor in the Bithynian Olympus.

This species occurs at altitudes of from 500 to 2650 m, in open places among rocks, herbs, or shrubs, sometimes in bogs, mostly in limy soil. Braun-Blanquet and Rübel (1484) state that in the middle E. Swiss Alps it occurs in open coniferous woods on detritus of slides and streams mostly from 1200 to 2200 m alt.

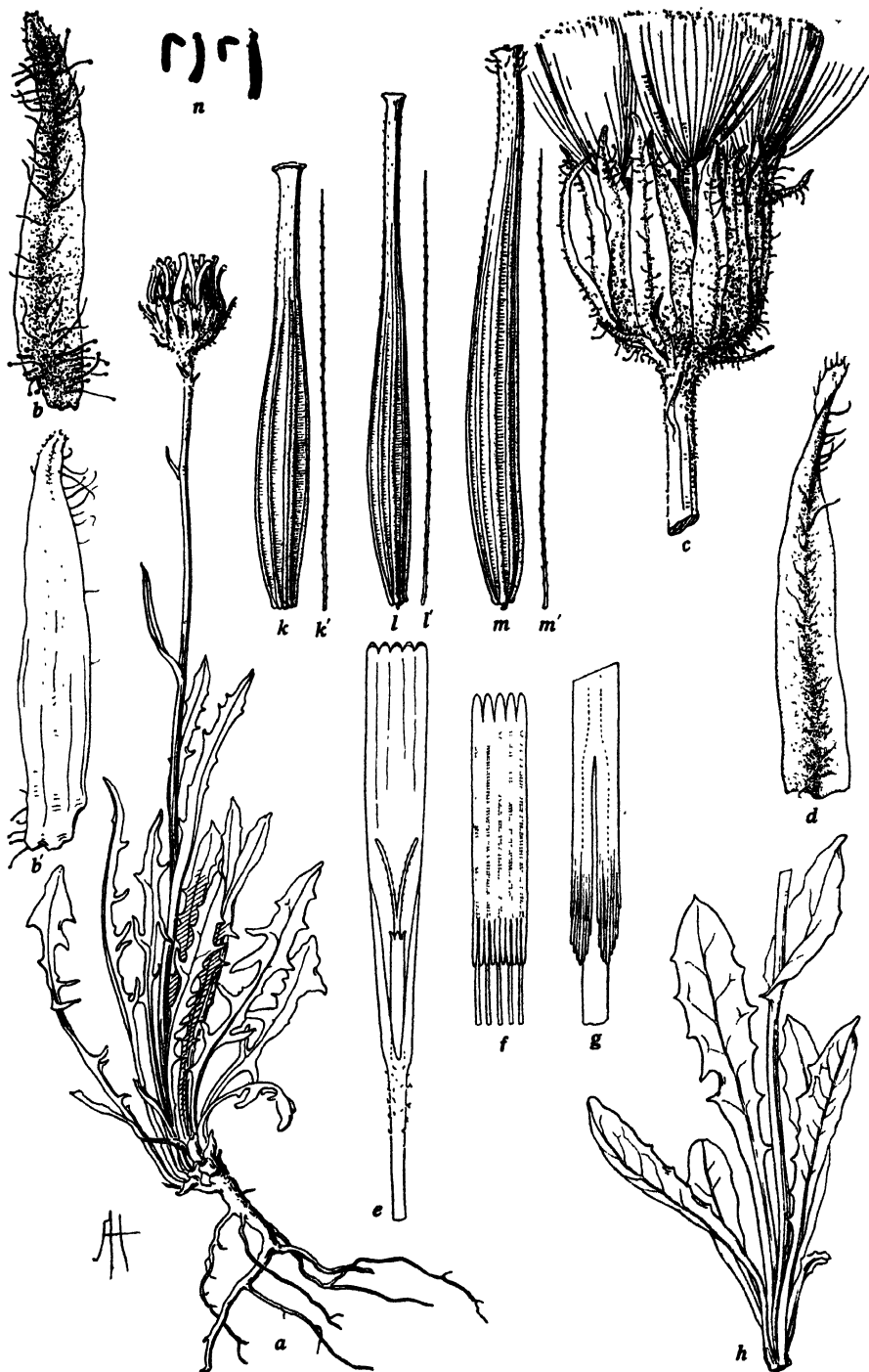


Fig. 59. *Crepis alpestris*, a-g, from Steininger 3404 (Minn 222745); h, from *C. Richter* (Minn 222746); k, from Reichenbach 1699 (Ms); l, from Schleicher (Po 10828); m, collector and place unknown (DC); n, from hort. genet. Calif. 2512 (seeds received from Lausanne Bot. Gard.): a, plant, $\times \frac{1}{2}$; b, b', inner involucre bract from (a), outer and inner sides, $\times 4$; c, head, with immature achenes, $\times 2$; d, inner involucre bract, outer side, from (c), $\times 4$; e, floret lacking ovary, $\times 4$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, lower part of a plant, $\times \frac{1}{2}$; k-m, achene and a pappus seta from 3 different plants (cf. m with fig. 4, taf. 98-I in Reichb. Ic. Fl. Ger. Helv. vol. 19); n, somatic chromosomes, $n = 4$, $\times 1250$.

The Tirolian spec. in Herb. Paris, labeled *H. alpestre* Jacq., is presumably authentic.

C. alpestris is fairly uniform with respect to the habit of the plant, which is characteristically 1-2-headed, although a plant with 4 or 5 long, 1-headed branches is rarely found. Many minor variations occur in size, leaf shape, and pubescence, and numerous varietal names have been recorded for such forms (cf. de Candolle, 166). But none of these forms seems to be of sufficient importance to call for its recognition as a taxonomic entity. However, the plant collected by Pichler in the Bithynian Olympus is of special interest, not so much because of a few distinctive floral features as because of its geographical location (cf. m.v. 1).

Switzerland: Canton Grisons, *Schleicher* (Po); Grisons, Albula, *Da Caruel* in 1891 (Fl); Grisons, between Crusch and Remüs, peat bogs on schist formation, *Briquet* in 1916 (Bur); Upper Engadine, above St. Moritz, *J. Ball* in 1873 (PA); Graubünden Alps, *Hegetschweiler* (UZ) as *C. longifolia*; Valais, vallée de Biun, Breithorn, 2650 m, *Cornaz* in 1894 (Bur); Schaffhausen, *Wolfabuct* in 1879 (Bur). **Germany:** Bavaria, Augsburg, Heidenviesen, *Weinhart* in 1885 (Minn); Bavaria, Isarauen, Wolfrathshausen, *Sandter* in 1887 (Po); Bavaria, Steingaden, *Neth* in 1899 (Minn); Upper Bavaria, Lechheide, Mering, alluvium and diluvium, about 500 m, *Eigner* in 1903 (Bur). **Austria:** Lower Austria, Gutenstein, *Richter* (Minn, Bur); Lower Austria, Schneeberg, *Keller* in 1886 (UC); Upper Austria, Stiria, Sonwendjoch, *Woynar* in 1887 (Minn); *ibid.*, near "Jungbauernalm," *Steininger* (Bur, Minn); Stiria, Tirol, collector? (P) as *Hieracium alpestre* Jacq., authentic (?). **Italy:** Tirol, near Pertisau, *J. Ball* in 1871 (PA); Seisser Alp, *Wolf* in 1896 (UC); Civezzano, *Gelmi* in 1880 (US); Longobardia, Sondrio Prov., Bormio, *Longa* in 1905 (Bur). **Turkey:** Bithynia, Olympus, *Pichler* in 1874 (K, MW, UWG, UWH) m.v. 1.

Minor Variant of C. alpestris

1. Ligules and anther tubes extremely broad and the filaments very short; ligules 3 mm wide; anther tube 4.75×1.5 mm dis.; filaments extending beyond appendages only 0.25 mm. Achenes not seen. It has not been possible to compare these differences in floral details with Pichler's material from Bulgaria. But these 2 collections are of importance in that they establish a present-day connection for this species between Asia Minor and S. central Europe, *Pichler* in 1874 (K, MW, UWG, UWH), Olympus, Bithynia, Turkey.

Relationship

Crepis alpestris is an outstanding species in that it is certainly related to other species both in central Europe (cf. *C. conyzaeifolia* and *C. blattarioides*) and in central and S. Africa (cf. *C. hypochaeridea* and *C. suffruticosa*). The collection of *C. alpestris* by Pichler in the Bithynian Olympus adds distributional evidence tending to support the evidence from morphology and cytology that the more primitive 4-paired *Crepis* species of central Europe and those of tropical and S. Africa were derived from a common stem which originated in Central Asia.

33. *Crepis suffruticosa* Babc.

Univ. Calif. Publ. Bot. 19: 403. 1941. (Fig. 60.)

Perennial, about 2 dm high; root woody, elongated; caudex strong, woody, divided, forming a small clump, the divisions short, thick, woody, covered with black bases of old leaves, leafy at crown; caudical leaves numerous, up to 11 cm long, 1.5 cm wide, oblanceolate, obtuse or acute, irregularly dentate, gradually attenuate into a winged petiole with broader clasping base, pubescent on both sides with fine pale hairs bearing brown glands, midvein prominent, purple; cauline leaves similar or acuminate, sessile, subamplexicaul, strongly dentate, teeth numerous, acuminate; stem erect or curved, terete, striate, fistulose, tomentulose, gland-pubescent or setulose above, remotely branched from near base or only at summit, aggregate inflorescence a 3-4-headed cyme; peduncles 1-5 cm long, erect, rather stout, somewhat thickened at summit, 1-2-bracteate, canescent-tomentose, gland-

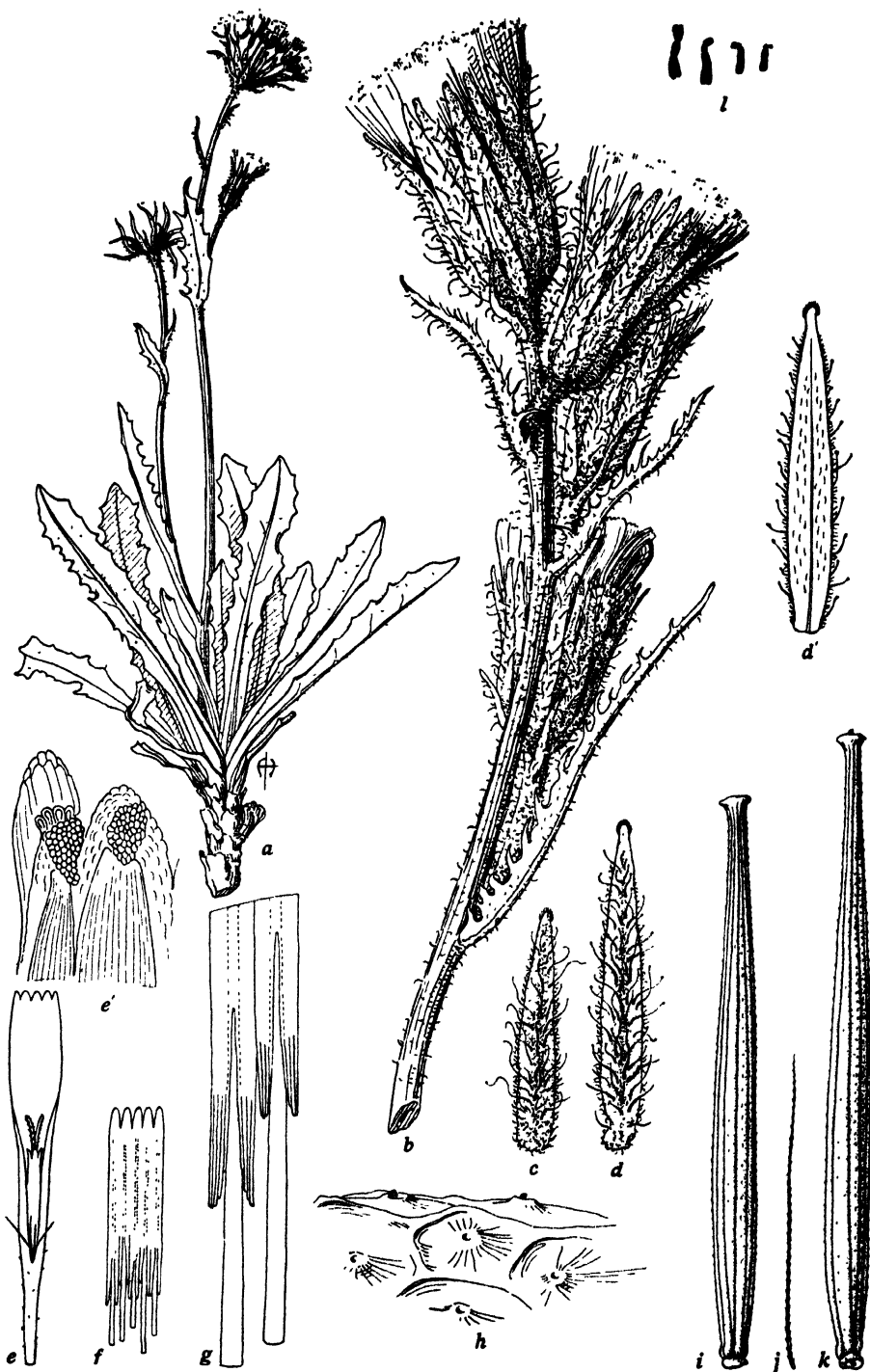


Fig. 60. *Crepis suffruticosa*, from type (K): *a*, plant, $\times \frac{1}{2}$; *b*, heads, $\times 2$; *c*, *d*, outer and inner involucral bracts, outer face, $\times 4$; *d'*, inner bract, inner face, $\times 4$; *e*, floret lacking ovary, $\times 4$; *e'*, detail of ligule teeth, $\times 50$; *f*, anther tube, $\times 8$; *g*, detail of appendages, $\times 32$; *h*, detail of receptacle, $\times 25$; *i-k*, 2 achenes and a pappus seta, $\times 8$; *l*, somatic chromosomes, $n = 4$, $\times 1250$.

pubescent and black-setulose; heads erect, rather large, many-flowered; involucre campanulate, about 15 mm long, 6–8 mm wide at base in fruit, canescent-tomentose, densely gland-pubescent with short pale hairs and longer black setules; outer bracts 8, with 2 or 3 subtending ones, unequal, longest $\frac{1}{2}$ – $\frac{2}{3}$ as long as inner bracts, lanceolate, obtuse, ciliate at tip, appressed-pubescent on inner face; inner bracts 12–16, innermost broadly membranous-margined, mediodorsally nerved, the nerve becoming indurate but little changed at maturity, ultimately reflexed, and then obviously pubescent on inner face with appressed white hairs; receptacle convex, 5–6 mm wide, areolate, glabrous; corolla 13 mm long; ligule 1.75 mm wide; teeth 0.2–0.3 mm long; corolla tube 3.5 mm long, stout, sparsely beset with clumps of 2-celled trichomes 0.1 mm long, the basal cell broad, greenish, the apical cell acicular, hyaline, also, at summit of tube *within*, pubescent with slender tortuous several-celled hairs up to 1.5 mm long; anther tube about 3.5×1 mm dis.; appendages unequal, 0.6–1 mm long, mostly 0.8 mm, lanceolate, acuminate; filaments unequal, 0.4–1 mm longer; style branches 1.1 mm long, 0.1 mm wide, rounded at apex, yellow; achenes chestnut brown, 9.5–10.5 mm long, 0.75 mm wide, subterete, gradually attenuate upward or coarsely beaked, summit 0.25–0.3 mm wide, with pale pappus disk about 0.5 mm wide, constricted above the oblique hollow pale-calloused base, 10-ribbed, ribs nearly equal, rounded, densely and finely spiculate from base to apex; pappus yellowish-white, about 6 mm long, 2-seriate, unequal in coarseness and length, rather fine, soft, persistent. Flowering Sept.; flowers deep yellow. Chromosomes, $2n = 8$.

Known only from the type locality, where it was reported by the collector as not common; hence, apparently, an extremely local endemic.

Monomorphic.

Tanganyika Terr.: Arusha Prov., Mt. Meru, sandy lava scree, 3787 m, B. D. Burtt 4060, Sept. 9, 1932 (K) type; cultivated from seed from type, hort. genet. Calif. 34.3281 (UC).

Relationship

Crepis suffruticosa is certainly related to *C. kilimandscharica* and its close allies, but is very distinct from them in the low stature, and from all except *C. kilimandscharica* and *C. caudicalis* in the suffruticose habit; also, in the glandular pubescence, smaller florets, and anther tubes which have narrow, unequal appendages, in the appressed hairs on inner face of the involucre bracts, in the naked receptacle, and in the shape of the achenes. The long hairs at the summit of the corolla tube, although more obscure than in *C. kilimandscharica*, also indicate relationship with that species; and the 2 species have closely similar karyotypes. At the same time, the habit, stature, and scapelike stems, with few large heads, in this relic species, are all reminiscent of *C. alpestris* and suggest a common origin for these African and Eurasian species. Although the karyotype of *C. suffruticosa* does not correspond as closely with that of *C. alpestris* as does that of *C. hypochaeridea*, yet there is a general similarity which is consistent with the hypothesis of a common origin.

34. *Crepis iringensis* sp. nov.

(Fig. 61.)

Herba perennis 3–6 dm alta; caudex rectus 2 cm latus ligneus superne foliatus; folia caudicalia numerosa suberecta ad 26 cm longa 3.5 cm lata lanceolata vel oblanceolata acuta vel acuminata retrorse denticulata petiolata superne glabra subtereglanduloso-setulosa; folia caulina plerumque parva ad basim dilatato-laciniata; caulis erectus robustus setulosus; inflorescentia aggregata cymoso-corymbiformia, ramis paucis oligocephalis; capitula magniuscula multiflora; involucre campan-

ulata 11–13 mm longa tomentulosa eglanduloso-setulosa; squamae exteriores circa 10 inaequales lineares, interiores 14–18 lanceolatae acutae ad maturitatem valde carinatae et ad basim spongioso-incrassatae; receptaculum alveolatum ciliatum; corolla circa 18 mm longa, ligula 13 mm longa 2.25 mm lata flava, tubo pubescenti, pilis acicularibus; antherae 5 mm longae; rami styli 2.25 mm longi flavi; achaenia fusca 6–7 mm longa 0.75 mm lata gradatim attenuata circa 12-costata; pappus pallido-flavidus 6–8 mm longus 2-seriatus persistens.

Perennial, 3–6 dm high; root vertical, woody, elongated; caudex at least 5 cm long, 2 cm wide, woody, covered with black bases of old leaves, simple, leafy at crown, 1–2-stemmed; caudical leaves numerous, ascending, up to 26 cm long, 3.5 cm wide, lanceolate or oblanceolate, acute or acuminate, retrorsely dentate, gradually attenuate into a winged petiole, with broader clasping base, glabrous on upper face, setulose on lower face, especially on midvein, with yellow glandless setules; lowest cauline leaf similar to caudical ones, the others all reduced, linear, with broader rounded laciniate base, or bractlike; stem rather stout, up to 5 mm wide near base, erect or sinuate, terete, sulcate or striate, sparsely setulose with yellow setules near base and black ones above, \pm fistulose, at least above, 1-branched from near base, this branch elongated, strict, few-headed, or branched only above, aggregate inflorescence cymose-corymbiform; peduncles 0.5–4 cm long, rather stout, arcuate, bracteate, tomentulose, setulose; heads erect, rather large, many-flowered; involucre campanulate, 11–13 mm long, 7–10 mm wide at base, tomentulose, setulose, with black or brown glandless setules; outer bracts about 10, often with 3–4 subtending ones, unequal, longest $\frac{1}{2}$ as long as inner bracts, 0.4–0.7 mm wide at base, linear, glabrescent, brown, scarious, becoming lax; inner bracts 14–18, lanceolate, acute, white-ciliate at apex, membranous-margined, ventrally glabrous, mediodorsally nerved, becoming carinate and somewhat but not conspicuously spongy-thickened at base in mature fruiting heads; receptacle alveolate, fimbriellae low, membranous, finely ciliate; corolla about 18 mm long; ligule 2.25 mm wide; teeth 0.4–0.7 mm long; corolla tube 5 mm long, pubescent from base to lower part of ligule with minute (0.05–0.2 mm long) acicular hairs; anther tube about 5×1.25 mm dis.; appendages 0.8 mm long, oblong, obtuse, truncate or notched; filaments 1 mm longer; style branches 2.25 mm long, 0.15 mm wide, attenuate, yellow; achenes brown, 6–7 mm long, 0.75 mm wide, laterally compressed, gradually attenuate to summit, which is about $\frac{1}{2}$ as wide as body and notably pale just below the slightly expanded pappus disk, constricted above the pale-calloused hollow base, about 12-ribbed, ribs nearly equal, rounded, finely muriculate or obscurely spiculate toward apex; pappus pale yellowish-white, 6–8 mm long, 2-seriate, unequal in length, rather fine, soft, persistent. Flowering Aug.–Mar.; flowers bright yellow.

E. Africa, Tanganyika Terr., Iringa Prov., Rungwe reg., W. Mporotos Mts., 1875–2300 m alt., in grassland associations, on black volcanic soil, especially on roadside banks; frequent to common.

Monomorphic.

Mt. Rungwe Dist.: in *Smithia-Polygala-Hyparrhenia* grassland, 2121 m, *Greenway 3543* (UC 513247) type; *ibid.*, *Greenway 3543a* (UC). **Mt. Mbeya Dist.:** above Mporoto sawmill, N. slope, *E. W. de H. 926* (K).

Relationship

Although *Crepis iringensis* is obviously related to *C. kilimandscharica* and its close allies, this species is distinct from all the other members of this group in the carinate and spongy-thickened inner involucral bracts and the shorter, less attenuate achenes, also in the finely ciliate fimbriellae of the receptacle and the densely

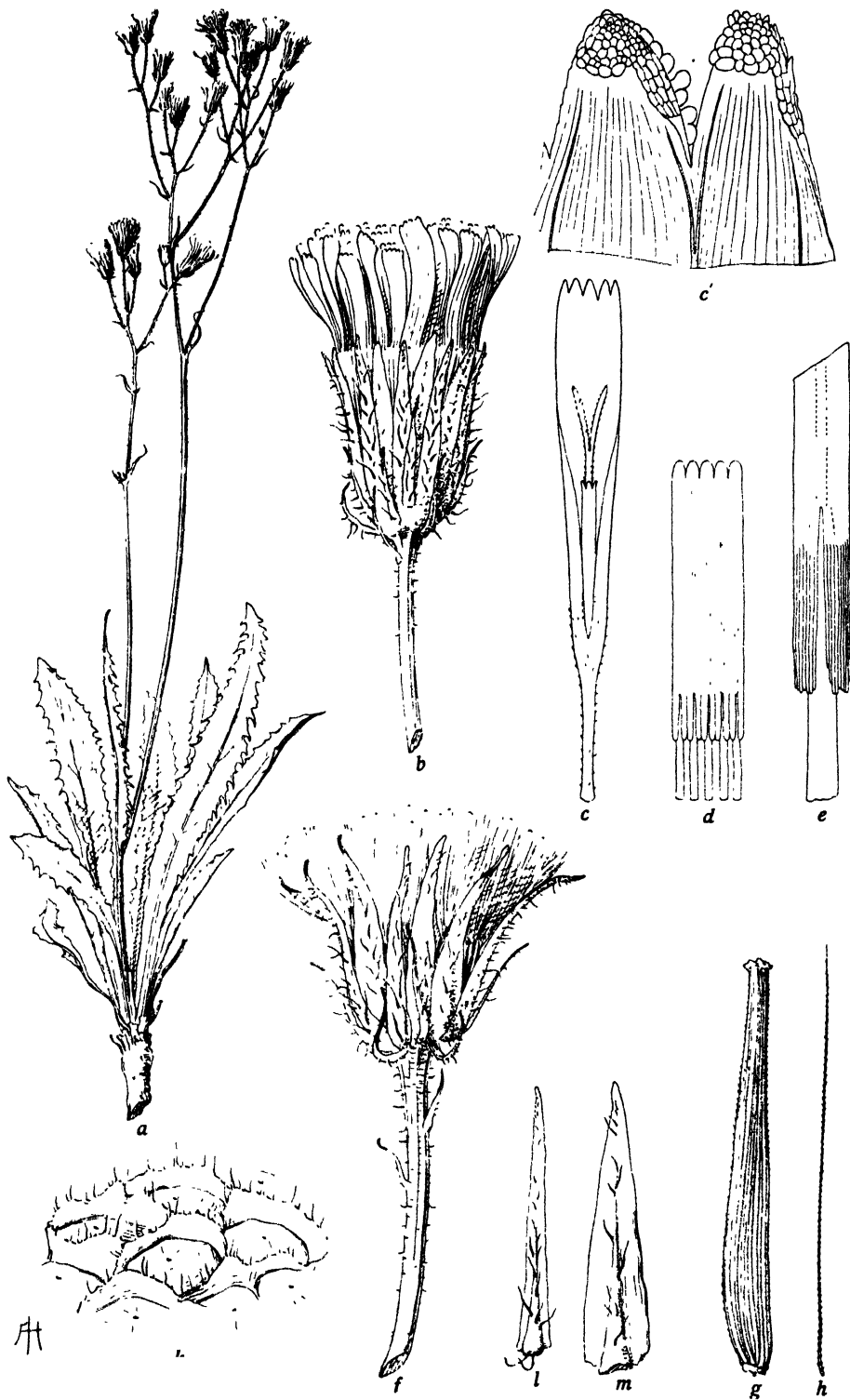


Fig. 61. *Crepis iringensis*, a-h, from type (UC 513247); k-m, from isotype (UC 513245): a, plant, $\times \frac{1}{4}$; b, flowering head, $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule teeth, $\times 50$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, fruiting head, $\times 2$; g, h, achene and pappus seta, $\times 8$; k, detail of receptacle, $\times 25$; l, m, 2 inner involucre bracts, outer face, $\times 4$.

pubescent corolla tube. The spongy-thickened involucre is generally a characteristic of more advanced species. But, even in the more primitive African species of *Crepis*, this character appears in a few instances. This group of closely related species shows nearest affinity with *C. hypochaeridea* and *C. Newii* and their relatives. They are less close to *C. scaposa*, *C. carbonaria*, and the other low-growing or otherwise reduced African species.

35. *Crepis meruensis* comb. nov.

(Fig. 62.)

Herba perennis 2–6 dm alta; radix recta tenua lignea; caudex 1–4 cm longus inflatus superne foliatus; folia caudicalia numerosissima erecta ad 25 cm longa 2 cm lata anguste oblanceolata obtusa acuta vel acuminata apiculata dentata vel denticulata glabra in petiolum alatum gradatim attenuata; folia caulina pauca remota similia vel linearia; caules 1–3 erecti fistulosi glabri superne ramosi, ramis paucis remotis elongatis 1–3-cephalis; inflorescentia aggregata cymoso-corymbiformia; capitula magna multiflora; involucre cylindrico-campanulata ad 15 mm longa ad basim 5 mm lata in fructu; squamae exteriores 8–10 inaequales lanceolato-lineares, interiores 12–15 lanceolatae obtusae ventraliter glabrae in fructu non incrassatae; receptaculum areolatum; corolla ad 18 mm longa, ligula circa 13 mm longa 2 mm lata flava saturata, tubo glabro; antherae circa 4.75 mm longae; rami styli 1.75 mm longi valde exserti flavi; achaenia fusca 7–9 mm longa 0.75 mm lata leviter compressa valde attenuata 10-costata; pappus pallido-flavidus 7 mm longus 2-seriatus persistens.

Perennial, 2–6 dm high; root vertical, slender, woody; caudex 1–4 cm long, ± swollen, covered with brown bases of old leaves below, leafy above; caudical leaves very numerous, erect, up to 25 cm long, 2 cm wide, narrowly oblanceolate, obtuse, acute or acuminate, apiculate, sinuate-denticulate or dentate, teeth often retrorse, gradually attenuate into a broad or narrow winged petiole, with broader clasping base, glabrous on both sides, midvein dark, rather prominent; cauline leaves few, remote, similar to caudical leaves or linear, sessile, uppermost bractlike; stems 1–3, erect, slender or rather stout, terete, fistulose, striate, glabrous, branched usually above middle, branches few, remote, elongated, 1–3-headed, aggregate inflorescence cymose-corymbiform; peduncles erect, stout, bracteate, slightly thickened near head in fruit, fuscous-tomentose, pubescent with short black gland hairs; heads erect, large, many-flowered; involucre cylindric-campanulate, up to 15 mm long, 5 mm wide near base in fruit; outer bracts 8–10, unequal, longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as inner bracts, lance-linear, like inner bracts tomentose and ± pilose with long black glandless hairs; inner bracts 12–15, lanceolate, obtuse, ciliate at tip, glabrous on inner face, not much changed in fruit, ultimately reflexed; receptacle areolate-fimbriate, areoles 0.5–1 mm wide, elevated with central depression, fimbriae low, membranous; corolla in marginal florets about 18 mm long; ligule 2 mm wide; ligule teeth 0.2–0.4 mm long, obtuse; corolla tube 4.5 mm long, wholly glabrous; anther tube about 4.75×1 mm dis.; appendages 0.5 mm long, oblong, obtuse; filaments 1.25–2 mm longer; style branches 1.75 mm long, 0.15 mm wide, attenuate, well extruded in anthesis, yellow; achenes brown, 7–9 mm long, 0.75 mm wide, lightly compressed, oblong, strongly attenuate upward, with slightly expanded pappus disk, somewhat constricted near the pale-calloused base, 10-ribbed, ribs nearly equal, narrow but rather prominent, some extending to summit, rounded, finely muriculate under lens; pappus pale yellow, 7 mm long, rather coarse, 2-seriate, united at base, persistent. Flowering Oct.–Feb.; flowers deep yellow.

Crepis kilimandscharica O. Hoffm. var. *meruensis* R. E. Fr., Svensk Bot. Tidskr. 22: 356, 1928.

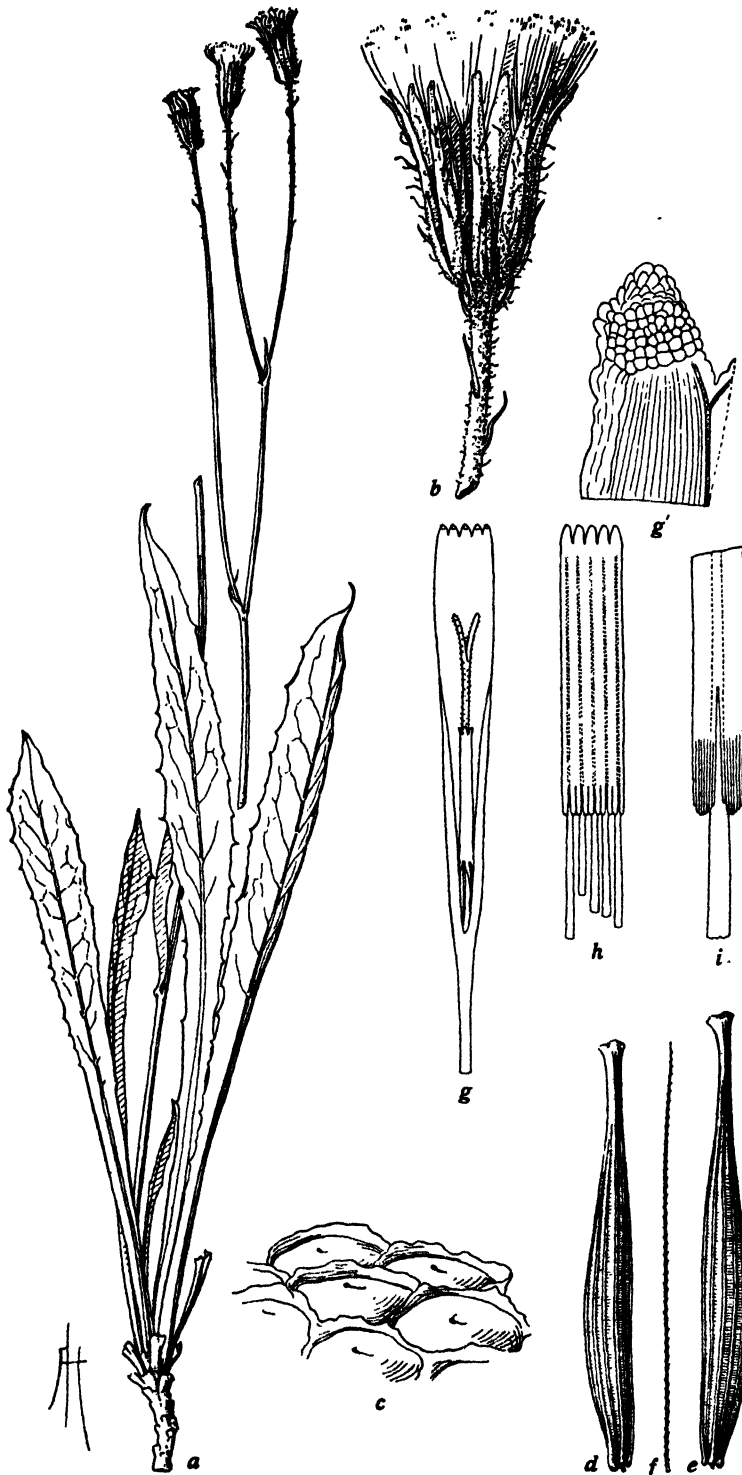


Fig. 62. *Crepis meruensis*, a-f, from type (Stockholm); g-i, from Uhlig 620 (B): a, plant, $\times \frac{1}{2}$; b, head, $\times 2$; c, detail of receptacle, $\times 25$; d-f, 2 achenes and a pappus seta, $\times 8$; g, floret lacking ovary, $\times 4$; g', detail of ligule teeth, $\times 50$; h, anther tube, $\times 8$; i, detail of appendages, $\times 32$.

E. Africa, Tanganyika Terr., Mt. Meru and Mt. Kilimanjaro, 2000–4000 m alt.; on grassy strips above virgin forests, on moist walls of ravines, and in rock clefts of lava dykes.

Meru: 3500–4000 m, *Sjöstedt* in 1906 (Stockholm) type; Meru, above Arusha, 2900 m, *Uhlig 620* (B, Amani); Meru, crater, 3484 m, *Burt 4148* (K). **Kilimanjaro:** Marangu, 2000 m, *Grote 6230* (Amani) m.v. 1; Kilimanjaro, below Peter's hut, 3666 m, *Greenway 3745* (UC) m.v. 2.

Minor Variants of C. meruensis

1. Caudex much swollen; caudical leaves shorter and narrower than in the typical form; achenes (immature) more strongly attenuate. *Grote 6230* (Amani) 2000 m, Marangu, Mt. Kilimanjaro.

2. Involucre and adjacent peduncle more densely hirsute, leaves as in m.v. 1; mature achenes lacking. *Greenway 3745* (UC) 3666 m, below Peter's hut, Mt. Kilimanjaro.

Relationship

Crepis meruensis is closest to *C. keniensis* and *C. kilimandscharica*. With the latter it has been confused, but it is easily distinguished by the absence of an elongated caudex, by the wholly glabrous leaves, stems, and corolla, the narrow or linear cauline leaves, fewer heads, smaller florets, style branches, and anther tube, with much shorter appendages, shorter and less attenuate achenes, shorter pappus, and differences in the ligule teeth and receptacle. From *C. keniensis* (q.v.) it is also distinct, and the latter is found only on Mt. Kenya. *C. meruensis* is a comparatively low-growing herb with woody root and small caudex, whereas *C. kilimandscharica* is suffrutescent, having a strong woody caudex at least 20 cm long, the mature plant often reaching over a meter in height. The 2 species occur in different ecological associations.

36. *Crepis cameroonica* Babc.

Ex Hutchinson et Dalziel, Fl. W. Trop. Afr. 2(1): 178. 1931. (Fig. 63.)

Perennial, 2.5–5 dm high; root vertical, woody, strong; caudex 0.5–1.5 cm wide, simple or forked, covered with brown bases of old leaves; caudical leaves ascending, up to 20 cm long, 2.5 cm wide, oblanceolate, obtuse or somewhat acute, mucronate, retrorsely denticulate, attenuate into a winged petiole with broader clasping base, pubescent on both sides with short pale glandless hairs; lowest cauline leaves (near base) similar, middle ones reduced, lanceolate, acuminate, sessile, rounded-amplexicaul, uppermost bractlike; stem erect or ascending, terete, striate or sulcate, fistulose, sparsely pubescent, sometimes tomentulose at base of leaves, simple and 1-headed to 2–4-furcate and then an open 2–14-headed cyme; peduncles 5–17 cm long, somewhat lax, becoming rather stout and strict in fruit, canescent-tomentulose, 2–3-bracteolate, pubescent with short gland hairs, \pm setuliferous and somewhat broader near base of head; heads erect, rather large, many-flowered; involucre campanulate, 13–16 mm long, 5–10 mm wide at middle in fruit, tomentulose, setulose, with black or mottled setules sometimes bearing a small gland; outer bracts 10, unequal, longest $\frac{1}{2}$ as long as inner ones, lanceolate, acute; inner bracts 13, lanceolate, acute, pubescent on inner face, mediodorsally nerved, not much changed at maturity, ultimately reflexed; receptacle 6–8 mm wide, alveolate, fimbriellae strongly ciliate; corolla 15 mm long; ligule 1.25 mm wide; teeth 0.3–0.5 mm long; corolla tube 4 mm long, slender, pubescent with stout acicular hairs 0.1–0.4 mm long; anther tube 3.4×0.9 mm dis.; appendages 0.75 mm long, acute or obtuse; filaments 0.8 mm longer; style branches 1.4 mm long, less than 0.1 mm wide, yellow; achenes brown, 8–10 mm long, 0.7–0.9 mm wide, subterete, fusiform, gradually attenuate into a true beak equal to the body, beak paler, 0.15 mm wide, pappus disk 0.25 mm wide, narrowed to the pale-calloused hollow base, 10-ribbed, ribs

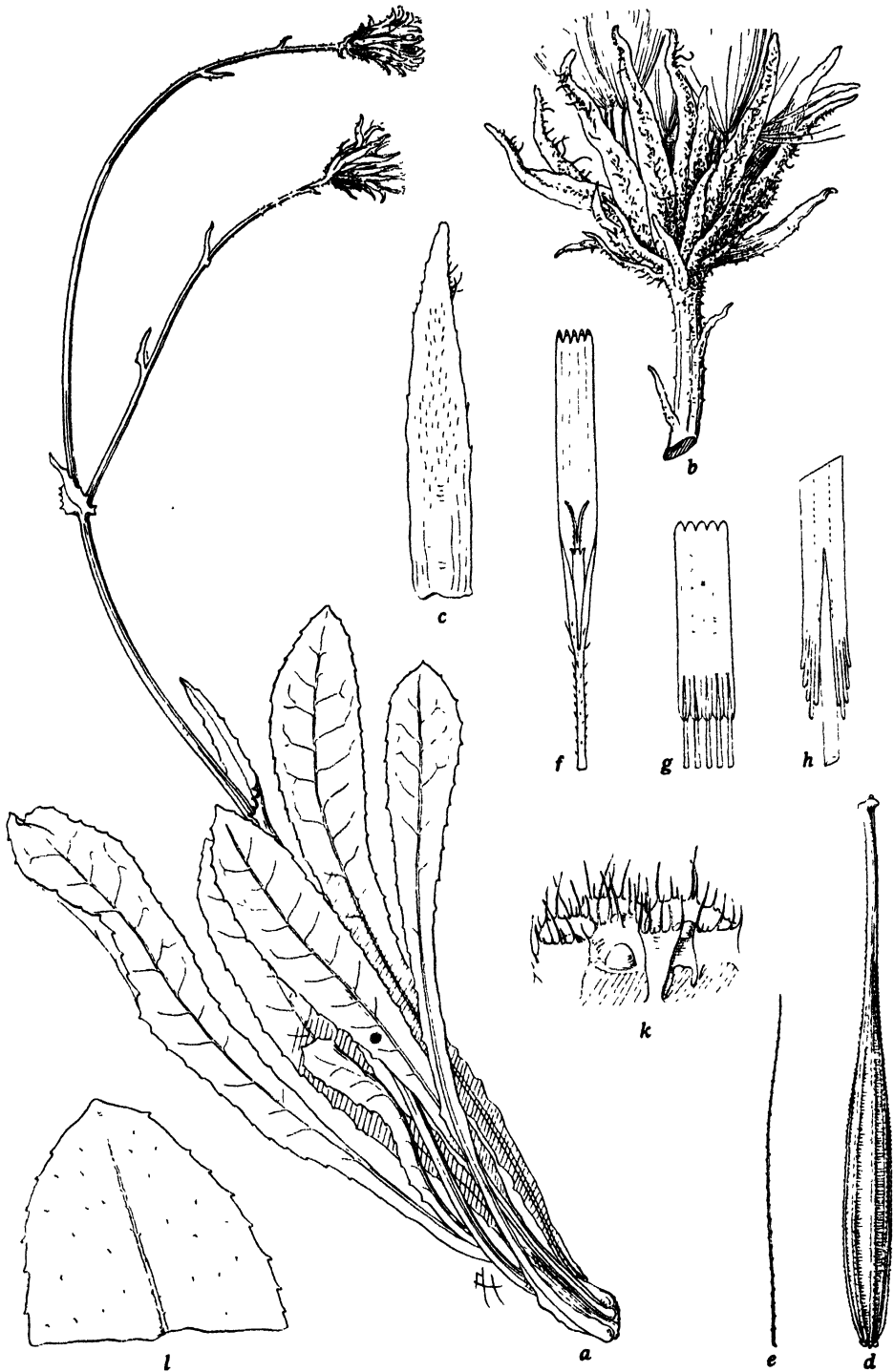


Fig. 63. *Crepis cameroonica*, a-c and f-k, from type (K); d, e, from Preuss 724 (Mu); l, from Mann 1918 (G): a, plant, $\times \frac{1}{2}$; b, fruiting head, $\times 2$; c, inner involucre bract, inner side, $\times 4$; d, e, achene and pappus seta, $\times 8$; f, floret lacking ovary, $\times 4$; g, anther tube, $\times 8$; h, detail of appendages, $\times 32$; k, detail of receptacle, $\times 25$; l, apical part of a caudical leaf, $\times 2$.

nearly equal, narrow, rounded, finely spiculate; pappus yellowish-white or pale tawny, 5–6 mm long, 2-seriate, rather fine, soft, persistent. Flowering Dec.–Feb.; flowers yellow.

Anisorhamphus hypochaeroides Hook. f., Jour. Linn. Soc. London, 7: 204. 1864, non *A. hypochaerideus* DC.

Crepis Hookeriana Oliv. et Hiern, Fl. Trop. Afr. 3: 450. 1877, non *C. Hookeriana* Ball.

Hieraciodes Oliverianum O. Kuntze, Gen. 1: 345. 1891 nom. nud.

W. tropical Africa, Cameroon, in mountain meadows from 2121 to 4090 m alt. Monomorphic.

Cameroon: Cameroon Mt., 2121 m, *Mann 1918* (K type, UCI); *ibid.*, 2121 m to summit, *Mann 1918* (K, G); locality (†), *Preuss 724* (Mu); *ibid.*, *H. H. W. 78* (K); Cameroon Mt., above Buea, grassland reg. above trees, about 2800 m, *Mildbraed 10886* (G).

Since Mann's original labels, as well as Mildbraed's, give "Cameroon Mountain" (not "mountains," as stated by Oliver and Hiern, *loc. cit.*), it seems probable that the other 2 specimens cited above were also collected on that mountain. At any rate, the type locality is definitely Cameroon Mt.

Relationship

C. cameroonica appears to be intermediate between *C. kilimandscharica* and its close allies and *C. hypochaeridea* and its near relatives. But in habit, character of receptacle, size of florets, and the ventral pubescence of the inner involueral bracts it shows closer affinity with *C. kilimandscharica*. The occurrence of this high montane endemic species on the W. coast of Africa either indicates that tropical Africa was once well populated with species of *Crepis* or necessitates the assumption that the seeds were transported from E. Africa by wind or by birds. This problem is discussed in Part I (pp. 134–136), where it is shown that transportation by either wind or birds is a reasonable assumption.

37. *Crepis Schultzii* (Hochst.) Vatke

Linnaea, 39(5): 514, 1875; ex Oliv. et Hiern, Fl. Trop. Afr. 3: 488. 1877. (Fig. 64.)

Perennial, 9–15 dm high; root not seen; caudex 7+ cm long, 1 cm wide, woody, covered with brown scaly bark, erect, 2–3-branched near summit, leafy at base of flower stem; stem of the current season's growth 5–8 mm wide near base, erect, terete, striate to strongly sulcate, fistulose, pale yellowish-green, scabrous with yellow glandless setae, leafy from base to summit, tomentose and setulose near inflorescence with black glandless setules; caudical leaves several, up to 25 cm long, 5 cm wide, oblanceolate, obtuse or acute, remotely denticulate, very gradually attenuate into a broadly winged petiole, scabrous on both sides with yellow glandless setiform hairs; lower cauline leaves similar, middle cauline leaves oblong, acute, sinuate-dentate, with triangular acute teeth, sessile, base rounded, subamplexicaul, scabrous, uppermost leaves gradually reduced, linear or bractlike; aggregate inflorescence a small rather dense few-headed corymbiform compound cyme; peduncles 1–4 cm long, slender, tomentose and black-setulose; heads erect, small, many-flowered; involucre campanulate, 7–8 mm long, 5–6 mm wide at middle in fruit, fuscous-tomentose at base, densely setulose and pilose, with black or green glandless and glandular hairs; outer bracts 8–10, unequal, $\frac{1}{2}$ – $\frac{2}{3}$ as long as inner bracts, subulate, acuminate; inner bracts 12–14, equal, lanceolate, obtuse and white-ciliate at apex, pubescent on upper half of inner face with yellow shining hairs, becoming indurate but not much changed at maturity; receptacle areolate-fimbriate, fimbriellae shortly and finely ciliate; corolla about 13 mm long; ligule 1–1.25

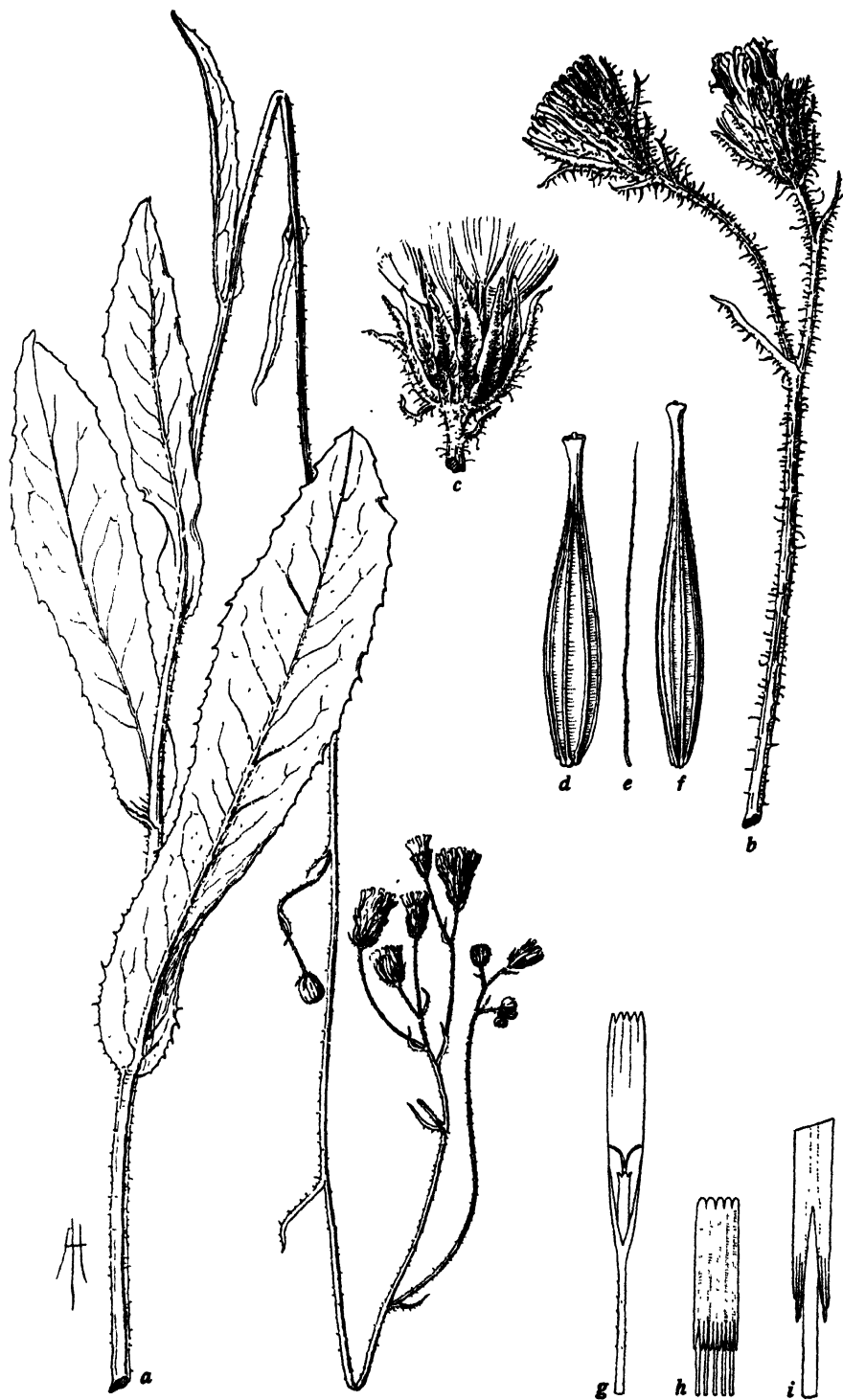


Fig. 64. *Crepis Schultzei*, from type collection (P, PC, UC 660574): *a*, plant lacking root, $\times \frac{1}{2}$; *b*, 2 flowering heads and peduncles, $\times 2$; *c*, fruiting head, $\times 2$; *d-f*, 2 achenes and a pappus seta, $\times 8$; *g*, floret lacking ovary, $\times 4$; *h*, anther tube, $\times 8$; *i*, detail of appendages, $\times 32$.

mm wide; teeth 0.2–0.3 mm or sometimes longer, acute; corolla tube 5 mm long, sparsely pubescent with stout acicular hairs 0.1 mm long; anther tube 2.6×0.75 mm dis.; appendages 0.5 mm long, lanceolate, acute; filaments 0.75 mm longer; style branches 0.75 mm long, yellow; achenes brown, 5.5–6 mm long, 0.8–1 mm wide, subterete, fusiform, strongly attenuate into a short beak about 0.2 mm wide, with swollen pale pappus disk 0.3–0.4 mm wide, constricted above the small pale-calloused base, 10–13-ribbed, ribs nearly equal, rounded, muriculate; pappus yellowish-white, 5–6 mm long, 2-seriate, fine, soft, deciduous. Flowering Nov.–Jan.; flowers yellow.

Crepis Schultzii Hochst., in Schimp., Pl. Abyss. II, 861 sine descr.

Barkhausia Schultzii Hochst., ex A. Rich., Fl. Abyss. 1: 464. 1847.

Brachyderea Schultzii Sch. Bip., ex Schweinf., Fl. Aethiop. 283. 1867.

Huraciodes Schultzii O. Kuntze, Gen. 1: 346. 1891.

N. Abyssinia, the region east and north of Lake Tana, in mountains at least up to 2400 m alt.

Monomorphic.

Abyssinia: Amhara-Tigre reg. (Semiène, acc. to Richard), Mt. Aber, near Adesela, forest, Schimper, iter Abyss. II, 861 (P type, PC, Bo, Fl, Ms, K, US, UC, B, Upsala, Stockholm) type collection; Tigre, Begemder, Schimper 1434 (K); "am Reppe," Schimper 1434 (US); mountain slope on Repp R., near Gerra Abuna Tekla Haianot, 2400 m (acc. to Fries, Svensk Bot. Tidskr. 22: 354), Schimper 1434 (K, B).

Relationship

Crepis Schultzii, a forestal species, is monomorphic as known at present. Although obviously related to *C. kilimandscharica* and its closest allies, yet it is very distinct in its tall stature and conspicuous cauline leaves combined with the small size of the heads and florets. The classification of this species under *Barkhausia* by Richard (*loc. cit.*) was based, no doubt, on the beaked achenes; but the involucre is essentially unchanged at maturity and the achenes resemble those of the more primitive *C. meruensis*.

38. *Crepis carbonaria* Sch. Bip.

Flora, 22: 19. 1839. (Fig. 65.)

Perennial, 1–3.5 dm high; root vertical, elongated, slender, woody; caudex 0.5–1 cm long, 1 cm wide, simple or 1-furcate, leafy; caudical leaves 5–15 cm long or longer in shade forms, up to 2 cm wide, obtuse or acute, apiculate, denticulate or rarely runcinate-dentate, attenuate into a short or long narrow petiole, glabrescent; lower cauline leaves often absent, when present similar to caudical leaves, middle and upper cauline leaves 1–3, lanceolate or linear, acuminate, pinnatifid, with narrow acuminate lateral segments, uppermost bractlike; stems 1–3, slender, erect, paniculately remotely 1–3-branched, 1–7-headed, glabrescent below, fuscous-tomentose and pubescent above with black setiform glandless hairs; peduncles 1–10 cm long, rather stout, slightly thickened near head, often 1-bracteate, densely fuscous-tomentose, black-hairy, erect in anthesis, strongly bent down in fruit; heads medium, many-flowered; involucre cylindric-campanulate, 10–14 mm long, 5–7 mm wide at middle in fruit; outer bracts 10, nearly equal, $\frac{1}{2}$ as long as inner bracts, light brown, lance-linear, obtuse, with a dorsal median row of short fine dark hairs, becoming lax; inner bracts 11–13, in 2 unequal ranks, inner ones longer and broader, lanceolate, obtuse, ventrally glabrous, dorsally tomentulose and pubescent with a median row of black glandless setiform hairs, not much changed at maturity; receptacle areolate (?), naked (?); corolla 5.5–6 mm long; ligule 0.6 mm wide; teeth 0.2 mm long; corolla tube 1.5 mm long, glabrous or with a few minute hairs



Fig. 65. *Crepis carbonaria*, from type (PC), except *b*, from topotype (PC): *a*, plant, $\times \frac{1}{2}$; *b*, peduncle and head, $\times 2$; *c*, inner involucre bract, dorsal face, $\times 4$; *d-f*, achenes and pappus seta, $\times 8$; *g*, floret lacking ovary, $\times 4$; *h*, anther tube, $\times 8$; *i*, detail of appendages, $\times 32$.

at base of ligule; anther tube 1.75×0.5 mm dis.; appendages about 0.4 mm long, narrow, acuminate; filaments 0.5 mm longer, slender; style branches 0.5 mm long, narrow, yellow; achenes (not fully mature) brownish-yellow, 5 mm long, 0.8 mm wide, subcompressed, fusiform, narrowed toward the hollow calloused base, similarly attenuate into a very coarse short beak, with expanded pappus disk, 10–13-ribbed, ribs narrow, with broader spaces between, rounded, finely spiculate to summit of beak; pappus pale yellow or yellowish-white, 4–5 mm long, 2-seriate, rather fine, stiff, persistent. Flowering Aug.–Sept. in N. Abyssinia, Dec.–Jan. on Kilimanjaro; flowers yellow.

Barkhausia carbonaria Richard, Voy. Abyss. 1: 465. 1847.

Brachydeera carbonaria Sch. Bip., ex Schweinf., Fl. Aethiop. 283. 1867.

Hieraciodes carbonarium O. Kuntze, Gen. 1: 345. 1891.

N. Abyssinia in Amhara and Tigre provinces, on the higher mountains, and on Mt. Kilimanjaro, Tanganyika Terr. This highly distinctive species varies somewhat in length of leaves and stem, as well as in number of heads per stem. Plants like the one shown in fig. 65 certainly grow in moist situations; whereas smaller specimens with shorter leaves and fewer heads probably came from drier or more exposed places.

The type collection, *Rueppell* in 1832 (not seen by me), is illustrated by Fries (347); the 2 plants in this collection show closer resemblance to Greenway's specimen (no. 3921) from Kilimanjaro in length of leaves, but they are more like Schimper's plants from Demerki in number of heads and length of peduncles. Greenway's other specimen from Kilimanjaro shows a tendency to have a small dorsal wing or cornicle near the tip of the innermost involucreal bracts which does not appear in his no. 3921. Also, in these 2 plants, the florets and achenes are slightly longer than in the Abyssinian specimens; but until more material from Kilimanjaro has been studied, it seems hardly necessary to recognize a different subspecies at the southern location. The type locality, "provincia Simen," apparently is equivalent to Mt. Buahit in the Amhara-Tigre reg. This statement is based on the following evidence: Richard (in 1847) cites one of Schimper's collections without date, giving the following location, "Prope Demerki in provincia Semiène"; Fries cites Schimper's 1838 collection with the following, "Demerki auf dem Berg Bachit" (= Buahit ?); Mt. Buahit stands just north of Ras Dashan in the Simen Mts., which are situated northeast of Lake Tana.

Abyssinia: Amhara-Tigre Prov., Mt. Bachit (= Buahit ?), near Demerki, *Schimper 1383*, Aug. 9, 1838 (PC, UCf) type; *ibid.*, Demerki, *Schimper 1150 and 1383* (K, B, P, PC, DL, Fl, Ms). **Tanganyika Terr.:** Mt. Kilimanjaro, Bismark Hill, 2878 m, moorland association (not at all common), *Greenway 3921* (Amani); Mt. Kilimanjaro, Peter's hut, 3726 m, *Greenway 3733a* (UC), with *C. scaposa afromontana*.

Relationship

Crepis carbonaria is close to *C. Ellenbeckii*, from which it is clearly distinguished by the long stems and larger heads, with more numerous and smaller florets, as well as by the characteristic black setae on both outer and inner involucreal bracts. It is less close to *C. scaposa* and *C. glandulosissima*, from both of which it is easily distinguished by the definitely though shortly beaked achenes, the yellowish pappus, and the rather long black hairs on peduncles and involucre; it differs also in other characters. It is farther removed from *C. tenerrima* of sec. 11 and *C. Rueppellii* of sec. 27, in both of which the achenes are more slender and longer beaked and which differ in many other features.

39. *Crepis Ellenbeckii* R. E. Fr.

Svensk Bot. Tidskr. 22: 359. 1928. (Fig. 66.)

Perennial, about 0.8 dm high; root 0.5–0.8 cm wide, oblique, woody, black, simple or furcate below caudex; caudex 0.5–1.5 cm wide, covered with black bases of old leaves, simple or divided, leafy at crown; caudical leaves 6–10 cm long, 0.8–1.5 cm wide, oblanceolate or lanceolate, acute or acuminate, sinuate-denticulate, glabrous or glabrescent on both sides or pilose beneath, especially on midvein and at margin, with yellow glandless setiform hairs; cauline leaves 1 or 2, with 1 subtending the 1–4-headed cyme and often exceeding the heads, linear, acuminate, \pm pilose; stems 3–5, ascending or semidecumbent, terete, striate, glabrous and woody at base, \pm pilose above, 1–2-furcate near summit, branches up to 1.5 cm long, erect in anthesis, densely fuscous-tomentose, \pm pilose; peduncles 0.3–0.5 cm long; heads small, 15–20-flowered; involucre cylindric-campanulate, in anthesis 8–10 mm long, 4–5 mm wide, dark green, tomentose at base, pilose or shortly setulose, glandless; outer bracts 5–7, nearly equal, $\frac{1}{2}$ as long as inner bracts in anthesis, 0.5–0.8 mm wide at base, linear, slightly attenuate, obtuse, glabrous or finely pubescent; inner bracts 9–13, oblong, the upper $\frac{1}{3}$ attenuate, very obtuse, ciliate at apex, glabrous on inner face, with a median dorsal row of black glandless setules, condition in mature fruiting heads not seen; corolla 9 mm long; ligule 1.25 mm wide; teeth 0.15–0.2 mm long; corolla tube 3.5 mm long, glabrous; anther tube 1.5×0.6 mm dis.; appendages 0.25 mm long, lanceolate, acute; filaments 0.25 mm longer; style extruded 1.5–2 mm, the branches 0.9 mm long, 0.1 mm wide, obtuse, yellow; mature achenes not seen; ovary constricted below the pappus disk; pappus yellowish-white, 4.5–5 mm long, 2-seriate, rather fine, soft. Flowering Mar.–May; flowers yellow.

The above description, including flower parts, is based on the 2 plants of the type collection. On the same sheet are fragments of inflorescence from 1 or more other plants. In these the stem, branches, peduncles, and involucre are closely similar to the type plants. The corolla, style, and style branches are also similar, but the anther tube is strikingly different in size, being about 3×1 mm when opened out. Such a great variation in otherwise typical material is unusual and it is of interest in connection with certain forms of this species (see m.v. 3–6).

E., W., and N. Abyssinia, S. Kenya, and N.E. Tanganyika Terr.; short grassland, from 1500 to 2600 m alt.

Variation in one important floral character, even in the type collection, has been noted above. In view of the apparently sporadic occurrence of this species in widely separated districts, it is not surprising to find a number of variants which exhibit more noticeable differences. Although some of these variants have been identified in herbaria as *C. carbonaria*, yet they all approach *C. Ellenbeckii* more closely (see m.v. 1–6). As pointed out by Fries, this species occurs at much lower altitudes than *C. carbonaria*.

Abyssinia: Harrar, Garu Muluta (= Mulata Mts.), meadow, *Ellenbeck* 570 (B) type; Motsha (northwest of Kaffa), Gallas highland, *Steudner* 417 (B) m.v. 1; Debra Tabor, Gaffat, *Steudner* 431b (B) m.v. 2. **Kenya:** Limuru, *Snowden* 561 (K) m.v. 5. **Tanganyika Terr.:** Kilimanjaro, Mashami, *Haarer* 183 (K) m.v. 3; Kilimanjaro, Meneka, *Greenway* 3358 (UC) m.v. 3; Kondoa-Irangi, Mbulu dist., Hanang or Guruwe (Gurui) Mt., *Burt* 2304 (K) m.v. 6; Ubugwe and Iraku, *Merker* 83 (B) m.v. 4.

Minor Variants of C. Ellenbeckii

1. Leaves only 4–6 cm long, 0.7–1 cm wide; stem nearly twice as long as leaves, the yellow hairs absent; instead, the peduncles and involucre have very short fine black glandless hairs; heads smaller than in type; involucre 7–8 mm long. The corolla is 8–9 mm long, with the corolla tube



Fig. 66. *Crepis Ellenbeckii*, from type (B): a, plant, $\times 1$; b, 2 heads, $\times 2$; c, d, 2 inner involucral bracts, outer face, $\times 4$; e, floret lacking ovary, $\times 4$; e', detail of ligule teeth, $\times 50$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, young floret, with ovary and pappus, $\times 8$.

glabrous, and the anther tube is 1.5 mm long; achenes lacking. *Steudner 417* (B) between Mofas, Motsha (and Gaiut ?), Gallas highland, W. Abyssinia.

2. Size of leaves, stem, and heads as in m.v. 1; yellow hairs absent, only the reddish-brown tomentum present on peduncles and short black hairs on involucre; involucre 7–8 mm long; corolla 8 mm long. Material very scanty. In a packet attached to the sheet with the specimen cited below are fragments of inflorescence having the same brown tomentum on the peduncles and similar involucre and florets; and 1 head contains partly mature achenes which are brown, about 5 mm long, and strongly attenuate at the summit; pappus pale yellow, about 5 mm long. When specimens with fruit have been collected at the type locality, they should be compared with this form. *Steudner 431b* (B) Gaffat, Debra Tabor, N. Abyssinia.

3. The yellow glandless hairs absent from leaves, stem, and peduncles; heads smaller than in type; involucre 7–8 mm long, 3–4 mm wide, canescent-tomentulose, devoid of black hairs; corolla 7–8 mm long, the tube and lower part of the ligule pubescent with papilliform or acicular hairs up to 0.5 mm long; anther tube 1.75–2.25 mm long; achenes (in *Greenway 3358*) light brown, 4.5–5.5 mm long, 0.4–0.5 mm wide, strongly attenuate upward with slightly expanded pappus disk, constricted at the narrow pale-calloused base, 10-ribbed, ribs nearly equal, finely muriculate; pappus yellowish-white, 4–5 mm long. Although these plants lack all the pubescence of the type except the dense tomentum on upper stem and peduncles, yet the caudex, leaves, and involucre bracts are typical of this species and there are approximately 13 inner bracts. Also, the florets, which approach the typical size of this species, are too small for *C. Rueppellii* and too large for *C. carbonaria*. Pubescence on the corolla tube is no more atypical than the large anther tubes found in certain other forms. *Haarer 183, 1031* (K) Mashami, Kilimanjaro; *Greenway 3358* (UC), very common, flowers lemon yellow, Meneka, S. slope of Kilimanjaro, 1350–1500 m, Tanganyika Terr.

4. The yellow glandless hairs absent; upper stem, peduncles, and involucre pubescent, with very short fine black glandless hairs; anther tube 2.5 mm long. The outer and inner involucre bracts are typical; the corolla is 8–9 mm long and the tube is glabrous; pappus pale yellow, 5 mm long, achenes lacking. *Merker 83* (B) Ubugwe and Iraku, German E. Africa (= Tanganyika Terr.).

5. Leaves irregularly dentate; yellow glandless hairs absent; peduncle and involucre tomentose and pubescent, with very short fine black glandless hairs; heads about 30-flowered; corolla tube and lower part of ligule pubescent; anther tube 3 mm long. The involucre is typical in length and in both outer and inner bracts, although a little broader than in the type; and the corollas are about 9 mm long. In this form we find combined the 2 most striking variations in this polymorphic species, viz., large anther tube and pubescence of corolla tube. *Snowden 561a* (K) Limuru, Kenya.

6. Heads broader than in the type, with more florets; both outer and inner involucre bracts pilose, with long black glandless setules; peduncles shortly pubescent and fuscous tomentose; corolla tube and base of ligule pubescent, with acicular hairs up to 1 mm long. Involucre 9 mm long, the outer and inner bracts typical in size and shape; corolla 11 mm long; anther tube nearly 2 mm long; pappus pale yellow, 5 mm long, 2 seriate; achenes lacking. The broader heads and long black setules of the involucre give a superficial appearance resembling *C. carbonaria* and suggest that these plants may be of hybrid origin. In stature and florets, however, they show more resemblance to *C. Ellenbeckii* and, until more collections with achenes are available, they may be referred to this species. *Burt 2304* (K), short grassland, in shade of rocks, 2575 m, Hanang or Guruwe (Gurui) Mt., Mbulu dist., Tanganyika Terr.

Relationship

C. Ellenbeckii is close to *C. carbonaria* from which it is best distinguished by the short stems bearing 1 or 2 narrowly linear leaves at the bifurcations which are near the summit, by the somewhat smaller heads usually with fewer florets, and by the much larger corolla. The anther tube also is often larger in *C. Ellenbeckii*, although it is not so in the 2 whole plants of the type collection. Possibly mass collections and cytogenetic research will result in the merging of these two species.

SUBSECTION B. PARVIFOLIATAE

40. *Crepis urundica* Babc.

Bull. Jard. Bot. Etat (Bruxelles), 14: 296. 1937. (Fig. 67.)

Perennial, 5–7.5 dm high; root vertical, woody, 4 cm long, 0.8 cm wide, strongly fibrous below; caudex slightly swollen, leafy at crown; caudical leaves up to 14 cm long, 4 cm wide, elliptical to oblanceolate, obtuse, irregularly denticulate or dentate, denticles corneous-mucronate, gradually attenuate into a short broadly winged petiole, with prominent midvein, pale, scabridulous on both faces with short pale gland hairs and glandless setae; cauline leaves few, small, remote, basal ones similar to caudical but narrower, acute, the others linear, sessile, uppermost bract-like; stems 1–3, rigidly erect, strongly sulcate, canescent-tomentulose, hispidulous below, hispid above with short black glandular setules, remotely branched from near base, branches elongated, strict, cymosely few-branched at summit, 2–5-headed; peduncles 1–8 cm long in fruit, stout, divaricate or arcuate, setuliferous, ± canescent-tomentose; heads few, erect, large, many-flowered; involucre cam-

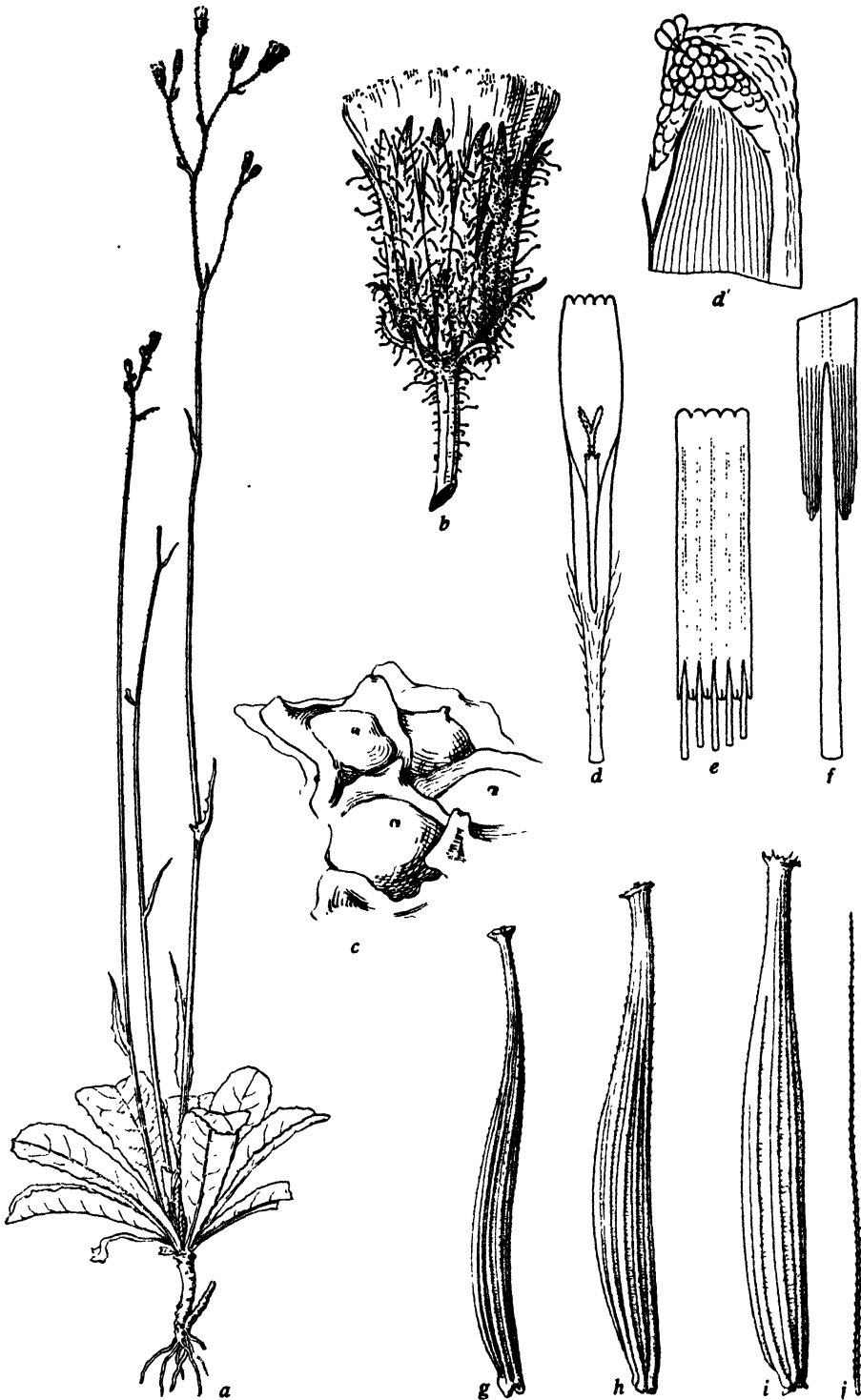


Fig. 67. *Crepis urundica*, from type (UC 545704): *a*, plant, $\times \frac{1}{4}$; *b*, head, $\times 2$; *c*, detail of receptacle, $\times 25$; *d*, floret lacking ovary, $\times 4$; *d'*, detail of ligule teeth, $\times 50$; *e*, anther tube, $\times 8$; *f*, detail of appendages, $\times 32$; *g-j*, 3 achenes and a pappus seta, $\times 8$.

panulate in fruit, 14–15 mm long, densely gland-setulose, \pm tomentulose, becoming lax or reflexed; outer bracts 8, unequal, longest $\frac{1}{2}$ – $\frac{2}{3}$ as long as inner ones, linear, lax; inner bracts 13–15, lanceolate, acute, glabrous and pale on inner face, narrowly carinate on outer face, becoming indurate but not spongy-thickened; receptacle areolate, naked; corolla 16 mm long; ligule 2.2 mm wide; teeth 0.15–0.3 mm long, obtuse; corolla tube 5 mm long, stout, white in sic., pubescent on upper $\frac{2}{3}$ with tortuous acicular several-celled hairs 0.05–1.25 mm long; anther tube 5×1.2 mm dis.; appendages 0.7 mm long, lanceolate, acute; filaments unequal, 0.6–1.2 mm longer; style branches 1 mm long, 0.2 mm wide, attenuate, yellow; achenes dark brown, 7.5–10 mm long, 1 mm wide, fusiform, straight, or somewhat curved, sub-compressed laterally or the marginal ones dorsoventrally, strongly attenuate to the apex or coarsely beaked, beak 1.5–2.5 mm long, pale, with slightly expanded pappus disk, constricted at the finely calloused hollow base, 10–12-ribbed, ribs nearly equal, rounded, finely spiculate, especially near apex; pappus pale yellow, 7.5–8 mm long, 1–2-seriate on the same fruit, rather coarse, persistent. Corolla pale yellow; anther tube and style branches deep yellow.

Known only from the type locality.

Monomorphic.

Belgian Congo: Urundi, Kisozi, cool moist places at base of hills, 2050 m, *Legrune* in 1936 (UC 545704) type, isotypes.

Relationship

Crepis urundica is intermediate morphologically between 2 fairly distinct groups, viz., the tall, large-headed, narrow-leaved species, represented by *C. kilimandscharica*, *C. mruensis*, *C. iringensis*, *C. keniensis*, and *C. cameroonica*, and the species characterized by shorter stature, small heads, and relatively broader leaves, represented by *C. Newii* and *C. Bruceae* of tropical Africa and *C. hypochaeridea* of S. Africa. From *C. kilimandscharica* and its close relatives, *C. urundica* is easily distinguished by its broader, elliptical, or oblanceolate leaves, by the glandular setules of peduncles and involucre, by various floral characters, of which the very short and broad style branches and the long, tortuous hairs on the corolla tube are most striking, and by differences in size and shape of the achenes. From *C. Newii*, *C. hypochaeridea*, and their allies, *C. urundica* is clearly set off by its taller, more robust habit, larger heads and florets, and again by the short and broad style branches and the pubescence of the corolla tube. *C. urundica*, therefore, is not only intermediate between 2 well-marked groups of African species, but it is also distinct from both in several distinguishing features. That it is very probably a diploid species is indicated by its pollen grains, which are 3-pored and regular in size and average $32\text{--}34\mu$ in diameter. In habit and leaf shape *C. urundica* definitely resembles the other species of subsection B, and it stands as the most primitive member of that group.

41. *Crepis hypochaeridea* (DC.) Thell.

Mitt. Bot. Mus. Univ. Zürich, 66: 255. 1921. (Figs. 68–70.)

Perennial, 1–3.5 dm high, with elongated woody taproot; caudex slightly swollen, simple, or 2–6-divided; caudical leaves semierect, oblanceolate or lanceolate, obtuse or acute, dentate to nearly entire, gradually attenuate into a short petiole with broader clasping base, \pm hispidulous on both sides with short erect yellowish glandless hairs or very short gland hairs or glabrescent, sometimes inconspicuously woolly within at base; cauline leaves small, linear, mostly bractlike; stems 1–3 to a caudex, striate, pubescent or tomentose or glabrate, not fistulose, few-branched or 1-headed, first branch often from near base, lower branches long,

1-3-headed, inflorescence cymose-corymbiform; heads erect, rather large, many-flowered; involucre 9-13 mm long, cylindric-campanulate in anthesis, broadly urn- or cup-shaped in fruit, like peduncles \pm tomentose and gland-pubescent, with or without dark green or black unequal setae; outer bracts 10, unequal, linear, acute, appressed or ultimately spreading, often pale, usually becoming purplish; inner bracts 12-14, lanceolate, obtuse, dark green, purplish and white-ciliate at tip, glabrous and strongly nerved on inner face, rarely reflexed in fruit, becoming indurate but not spongy-thickened at base, somewhat concave by inflection of the subscareous margins; receptacle alveolate; corolla 11-13 mm long; achenes dark brown at maturity, 6.5-10 mm long, subterete, fusiform, gradually attenuate into a coarse or rather fine beak, paler near summit, with expanded pappus disk, a white or yellowish callosity enclosing the hollow base, and 10-13 nearly equal, finely spiculate ribs; pappus 5-8 mm long, pale yellowish, soft, shining, 3-seriate, finely barbellulate, persistent. Flowers golden or chrome yellow.

The E. half of S. Africa from the Cape of Good Hope northward to Northern Rhodesia and Portuguese E. Africa; grasslands from 650 to 1800 m alt.

This species is somewhat variable in stature, size of leaves, and nature of the indumentum on involucre and leaves. Of greater significance are differences in habit of the plant and in certain features of the inflorescence and the achenes. Mainly on the basis of these latter variations, 3 subspecies may be recognized. A few types, some of which have been named previously as varieties, are listed as minor variants.

Key to the Subspecies of Crepis hypochaeridea

Plant usually 2-3.5 dm high (reduced forms sometimes 1.2-2 dm, but of typical habit); branches strictly erect or arcuate, not divaricate; achenes 1-1.2 mm wide, shortly beaked, the beak of mature marginal achenes about $\frac{1}{4}$ as long as the body, the summit abruptly expanded into the flat pappus disk or only slightly conical.

Outer involucre bracts longer, the longest $\frac{1}{2}$ as long as inner bracts; gland hairs on involucre dark, with brown glands; pappus 6-8 mm long 41, *a. genuina*

Outer involucre bracts shorter, the longest $\frac{1}{3}$ as long as inner bracts; gland hairs on involucre pale, with white glands; pappus 5-6 mm long 41, *b. rhodesica*

Plant 1-1.2 dm high; branches divaricate; achenes 0.75 mm wide, relatively longer beaked, the beak of mature marginal achenes about $\frac{1}{3}$ as long as the body, the summit long-conical 41, *c. brevicaulis*

41, *a. Crepis hypochaeridea genuina* (Thell.) comb. nov. Plant 1.5-3.5 dm high; leaves 4-11 cm long, up to 2 cm wide; stems 1-3, with 1-8 erect usually 1-headed branches; peduncles 1-25 cm long, setulose and tomentose near summit, or gland-pubescent and tomentulose; involucre 11-13 mm high, with dark green or black glandless setae, sometimes with short gland hairs and no setae; outer bracts unequal, longest $\frac{1}{2}$ as long as inner bracts; corolla 11 mm long; ligule 1.5 mm wide; ligule teeth 0.15 mm long; corolla tube 3.5 mm long, beset with stout or acicular 2-celled hairs up to 0.15 mm long arranged singly or in groups; anther tube about 4.5×1.1 mm dis.; appendages 0.75 mm long, narrow, obtuse; filaments stout, 0.75 mm longer; style branches 1.5 mm long, slender, yellow; achenes 7-9 mm long; pappus 6-8 mm long. Flowering Sept.-Dec. See fig. 68.

Anisorhamphus hypochaerideus DC., Prod. 7: 251. 1838: (*hypochaerideus*) Sonder, in Harvey et Sonder, Fl. Cap. 3: 530. 1864-1865.

Hieracium polyodon Fries, Epier. Hierac. 67. 1862; Sonder, loc. cit., 530. 1864-1865.

Crepis polyodon Phillips, Ann. South Afr. Mus. 16: 171. 1917.

Crepis hypochaeridea var. *Junodiana*, var. *Woodii* et var. *genuina* Thell., Vierteljahrsschr. Naturf. Ges. Zurich, 66: 255-256. 1921

C. Junodiana O. Hoffm., ex Thell., loc. cit.

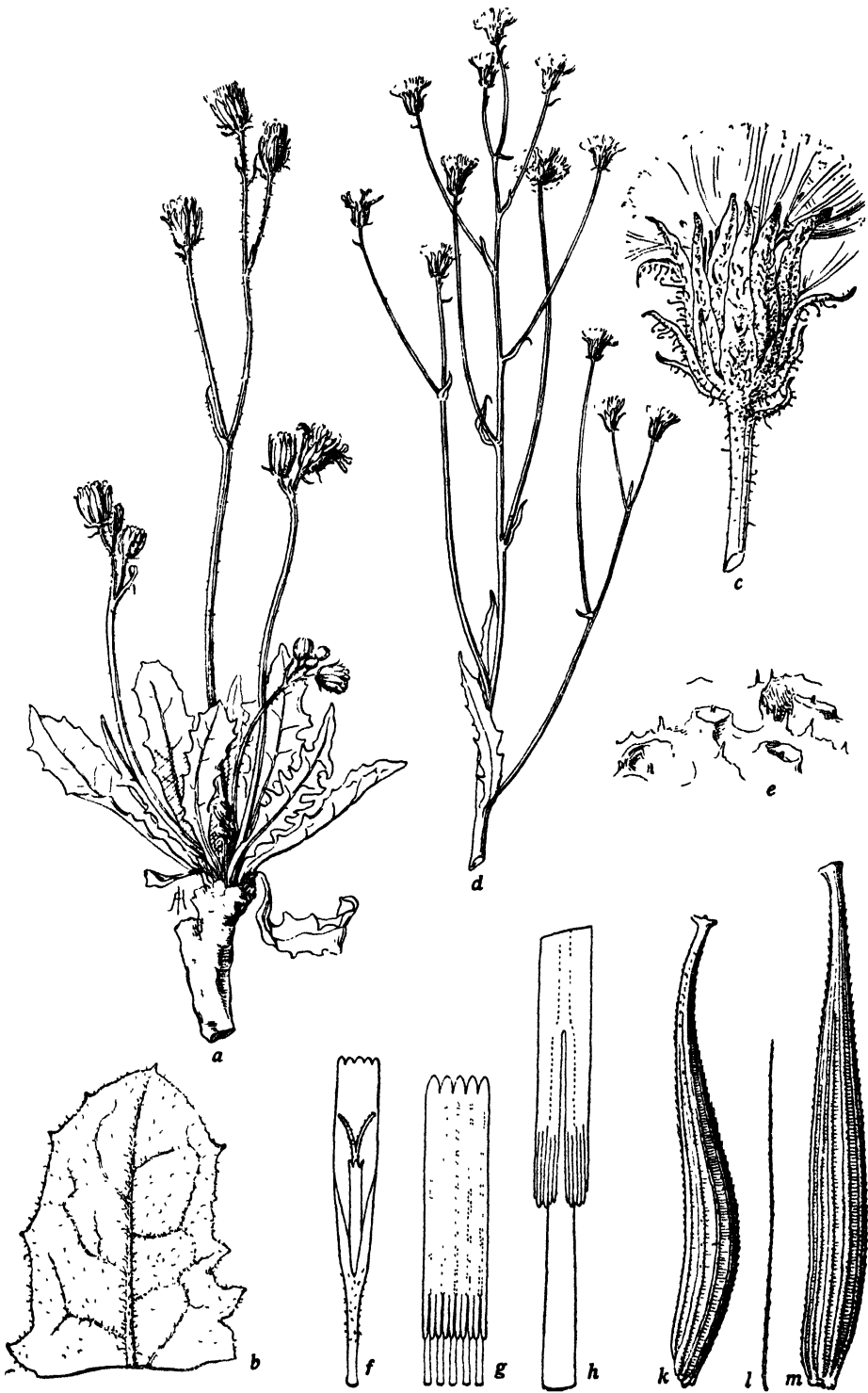


Fig. 68. *Crepis hypochaeridea genuina*, *a*, *b*, from Moss 15469 (UC 446476); *c*, from Moss 7388 (UC 446507); *d*–*m*, from Moss 6236 (Moss): *a*, plant, $\times \frac{1}{2}$; *b*, upper part of caudical leaf, lower side, $\times 2$; *c*, fruiting head, $\times 2$; *d*, upper part of aggregate inflorescence in a tall robust plant, $\times \frac{1}{4}$; *e*, detail of receptacle, $\times 25$; *f*, floret lacking ovary, $\times 4$; *g*, anther tube, $\times 8$; *h*, detail of appendages, $\times 32$; *k*–*m*, 2 achenes and a pappus seta, $\times 8$.

Union of South Africa from the Cape to the Transvaal and from Natal to Orange Free State.

Type locality unknown. In lieu of an authentic specimen of de Candolle, the collection of *Schlechter* in 1893, represented in 4 herbaria (UZ, K, BB, Ms), is accepted as typical. This is *C. hypochaeridea* var. *genuina* Thell., *loc. cit.*

Cape Province: Cape of Good Hope, *Armitage* in 1853 (Rome); Queenstown, Hangklip Mt., 1800 m., *Galpin* 1635 (K); Masube, *Jacottet* 21 (UZ); Mt. Boschberg (†), grassy places, 1500 m., *MacOwan* 1989 (UZ, K); Modderfontein, stony lanes, *Conrath* 547 (K). **Basuto Land:** Leribe, *Schlechter*, com. *Dieterlen* 500 (Ms, UC). **Griqua Land East:** Kokstad, *Tyson* 1097 (UZ, K); Kokstad, hills, 1600 m., *Tyson* 467 (K, G). **Natal:** Houtboschrand, grassy hills, 1400 m., *Schlechter* in 1893 (UZ, K, BB, Ms); Howick, near-by hill, 1200 m., *Wood* 5224 (UZ) m.v. 1; Howick, 1000 m., *Junod* 277 (UZ) m.v. 2; Inanda, *Wood* 207 (K); York, 1000–1300 m., *Wood* 4319 (K); Weenen Co., South Downs, 1600 m., *Wood* 4384 (K). **Orange Free State:** Harrismith, *Sankey* 115 (K). **Transvaal:** Lydenburg, *Wilms* 647 (UZ); Nelspruit, Schagen, hills, in long grass, *Liebenberg* 3296 (UC); Barberton, Saddleback Mt., 1300–1600 m., *Galpin* 1027 (K, UZ); Shiluwane, fields and hills, *Junod* 775 (K, UZ) m.v. 2; Johannesburg, Milner Park, *Moss* 6236 (Moss); *ibid.*, *Moss* 6237 (UC); Ashbury, near government nursery, *Repton* 314A (Pre); Johannesburg, Killarney, grass veld, *Ottley* 2251 (UC); Johannesburg, grass veld, *Moss* 7036 (UC) m.v. 3; Johannesburg, Melville, grass veld, *Moss* 7388 (UC) m.v. 3; Pietersburg dist., Woodbush Mts., grass veld, *Moss* 15469 (UC); Pretoria dist., Premier Mine, *Rogers* 23257 (UC).

Minor Variants of C. hypochaeridea genuina

1. (*C. hypochaeridea* var. *Woodii* Thell., *loc. cit.*) The indumentum of peduncles and involucre consists of long blackish setae. *Wood* 5224 (UZ) hill, 1200 m, near Howick, Natal.

2. (*C. hypochaeridea* var. *Junodiana* Thell., *loc. cit.*) The aggregate inflorescence is corymbiform; indumentum as in m.v. 1. *Junod* 277 (UZ) near Howick, 1000 m, Natal.

3. Leaves glabrous or minutely gland-pubescent, especially on midvein beneath; stems arcuate or flexuous, the branches sometimes 2-headed. *Moss* 7036 (UC) grass veld, Johannesburg, *Moss* 7388 (UC) grass veld, Melville, Johannesburg, Transvaal.

41, *b. Crepis hypochaeridea rhodesica* Babc., Univ. Calif. Publ. Bot. 19: 400. 1941. Plant 1.2–2(3) dm high; leaves 3–7 cm long, up to 2 cm wide, oblanceolate, broadly triangular at apex, narrowed into a broad membranous slightly auriculate base, repand-dentate or denticulate, pubescent on both sides with fine white hairs bearing white glands; stems 1–3, erect, 2–3-furcate, branches strictly erect at maturity, upper branches pedunculate, lower branches 1–2-headed; peduncles 4–14 cm long, gland-pubescent and tomentulose near summit; involucre 12 mm high, gland-pubescent, with short yellow hairs, glands white; outer bracts unequal, longest $\frac{1}{2}$ as long as inner bracts at maturity, ultimately spreading, pale or purplish, linear, acute; inner bracts lanceolate, acute, or obtuse, dark green, purplish and white-ciliate at apex, glabrous and nerved on inner face; receptacle alveolate; corolla about 13 mm long; ligule 1.5 mm wide; ligule teeth 0.2–0.3 mm long; corolla tube 5.25 mm long, slender, beset below with very stout papilliform hairs arranged singly or in groups, and above with acicular hairs up to 0.5 mm long; anther tube 3.7×1.3 mm dis.; appendages 0.75 mm long, oblong, sagittate; filaments stout, very short; style branches 1.5 mm long, 0.1 mm wide, yellow; achenes (7)8–10 mm long, 1–1.2 mm wide, slightly longer beaked than in subsp. *genuina*, otherwise similar; pappus 5–6 mm long. Flowering in the “pre-rain period”; the type was collected in December. Chromosomes, $2n = 8$. See fig. 69.

S.E. Southern Rhodesia and N.W. Northern Rhodesia; probably in the intermediate reg.

Southern Rhodesia: high veld, 1300–1600 m., *Walters* 2322 (K) type; Umtali, Manica, Odzani River valley, *Teague* 378 (K); Rusafu (Rusapi) *Heslop* (K); Zimbabwe, *Mrs. W. P. Cockerell* in 1931 (UC). **Northern Rhodesia:** Muinilunga dist., Matouchi farm, dry bank above Matouchi R., open situation, *Milne-Redhead* 1026 (K).

41, *c. Crepis hypochaeridea brevicaulis* Babco., Univ. Calif. Publ. Bot. 19: 401. 1941. Plant 1–1.2 dm high; leaves 3–7 cm long, up to 1.5 cm wide, oblanceolate, obtuse to acuminate, narrowed into a very short winged petiole with much broader clasping base, obscurely woolly at base within, repand-denticulate, puberulous on lower face with very short fine pale gland hairs or longer glandless hairs on midvein,

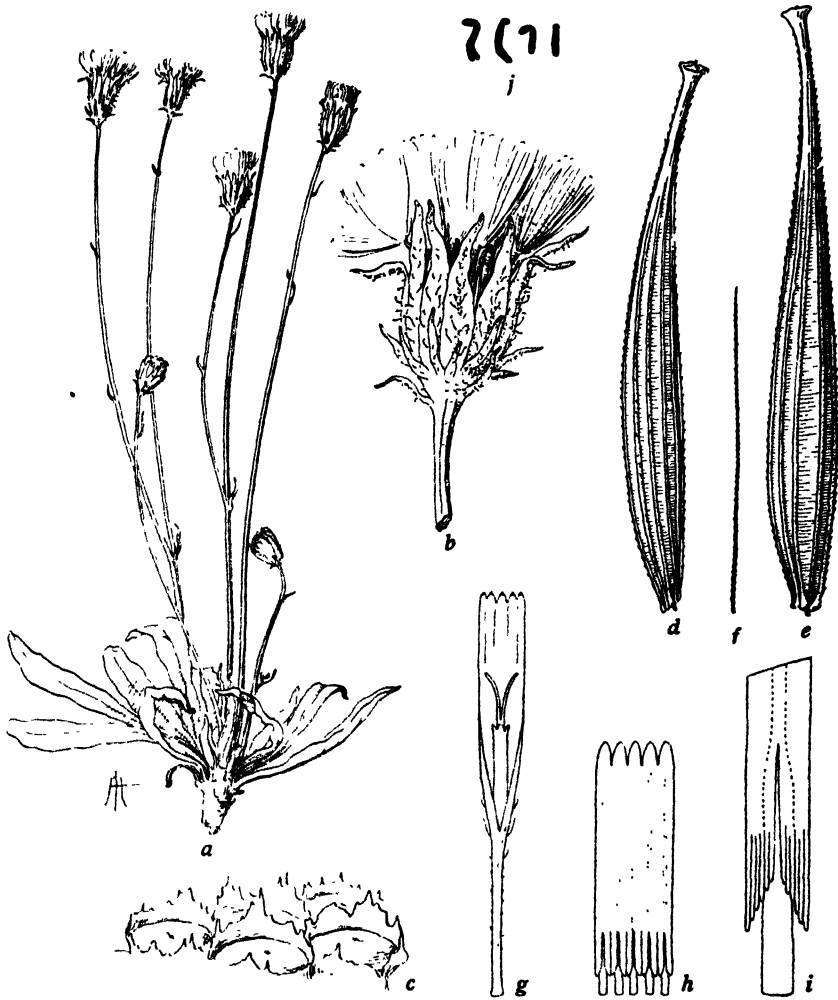


Fig. 69. *Crepis hypochaeridea rhodesica*, from type (K): a, plant, $\times \frac{1}{2}$; b, flowering head, $\times 2$; c, detail of receptacle, $\times 20$; d–f, 2 achenes and a pappus seta, $\times 8$; g, floret lacking ovary, $\times 4$; h, anther tube, $\times 8$; i, detail of appendages, $\times 32$; j, somatic chromosomes of seedlings grown from the type (hort. genet. Calif. 3059), $n = 4$, $\times 1250$.

or glabrescent; stems 1–3, erect or ascending, remotely 2–4-branched, lowest branch springing from the base, branches divaricate, 1–2-headed; peduncles 3.5–8 cm long, slender, 1–2-bracteate, gland-setulose or tomentulose near head; involucre 9–12 mm high, canescent-tomentose, gland-pubescent with short pale hairs bearing white glands, black-setulose; longest outer involucre bracts $\frac{1}{2}$ as long as inner bracts in fruiting heads, linear, becoming purplish and lax; inner bracts lanceolate, obtuse or acute, purplish and white-ciliate at apex, glabrous and nerved on inner face; receptacle alveolate; corolla 12–13 mm long; ligule 1.5 mm wide; teeth 0.2–0.4 mm long; corolla tube 4.5 mm long, sparsely beset with very short (up to 0.17 mm long)

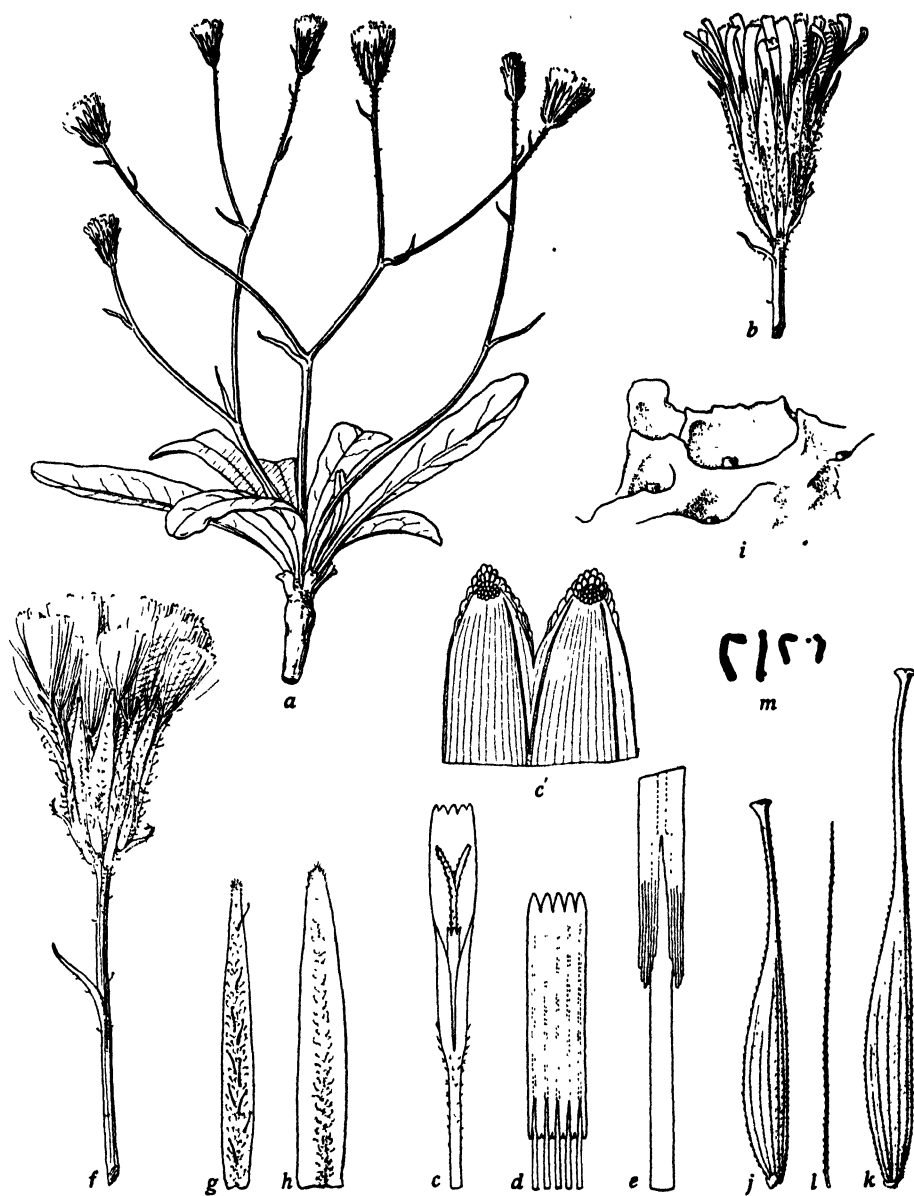


Fig. 70. *Crepis hypochaeridea brevicaulis*, from type and isotypes (UC 540739, 540738): a, plant, $\times \frac{1}{2}$; b, flowering head, $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule teeth, $\times 50$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, fruiting head, $\times 2$; g, h, 2 inner involucral bracts, outer face, $\times 4$; i, detail of receptacle, $\times 25$; j-l, 2 achenes and a pappus seta, $\times 8$; m, somatic chromosomes from seedlings grown from type collection (hort. genet. Calif. 3399), $n = 4$, $\times 1250$.

papilliform or acicular hairs arranged singly or in groups; anther tube 4×1 mm dis.; appendages 0.6 mm long, lanceolate, acute to obtuse; filaments 0.8 mm longer; style branches 1.2–1.5 mm long, 0.15 mm wide, acute, yellow; achenes 6.5–8.5 mm long, beak 2–3 mm long, the summit strongly obconical, pappus disk 0.4 mm wide, 12–13-ribbed; pappus 5.5–6 mm long. Flowering July. Chromosomes, $2n = 8$. See fig. 70.

Known only from the type locality, where it was observed to be very local.

N.E. Transvaal: Zoutpansberg Mts., Pisang Hoek, upper hill slopes, *Galpin* in 1935 (UC 540739) type.

Under cultivation in the greenhouse, plants of this subspecies had short stems and long, arcuate branches; stems and branches were purple-striate and the leaf midveins purple; ligules chrome yellow, anther tube and style branches yellow; and all the hairs or setules on the inner involucre bracts bore white or transparent glands. Apparently this subspecies is more nearly related to subsp. *rhodesica*, but it is distinct from that subspecies in the dwarf, spreading habit, longer outer involucre bracts, black setules on inner bracts, pubescence of corolla tube, long filaments of anther tube and narrower appendages, broader style branches, and shorter, narrower, and slightly longer beaked achenes with obconical apex.

Relationship

Crepis hypochaeridea is closest to *C. chirindica*, from which it differs in the much shorter stature of the plants in all 3 subspecies, the equal length of the inner involucre bracts and the broader outer involucre bracts, the larger florets and shorter anther appendages, and, subsp. *brevicaulis* excepted, especially in the shorter achenes with relatively shorter beaks. It is related also, but less closely, to *C. Newii bumbensis*. Through these 2 species, *C. hypochaeridea* is connected with all the *Crepis* species of tropical Africa. Distantly related Abyssinian species are the low-growing, thick-rooted *C. carbonaria* and the tall, leafy-stemmed forestal species, *C. Schultzei*.

The chromosomes of 2 of the 3 subspecies have been examined. They are closely similar and show general resemblance in size and shape to the chromosomes of 5 other African species. All 6 species have 4 pairs and there is general resemblance in the morphology of all 6 karyotypes. *C. alpestris* of the European Alps and Asia Minor also has 4 pairs of chromosomes which have a certain degree of resemblance to those of *C. hypochaeridea*, and the plant exhibits sufficient similarity to *C. hypochaeridea* to suggest that the two may have sprung from a common ancestral stock. *C. leontodontoides* of Morocco and Spain has 5 pairs of chromosomes and, even though still somewhat related, is farther removed phylogenetically.

Assuming that the Old World species of *Crepis* were derived from a Central Asiatic center, in accordance with Matthew's principle this African species of the south temperate zone would be fairly primitive. Its phylogenetic position in this monograph, which is based on comparative morphology, confirms this expectation. The numerous related species of tropical and N. Africa, some of which are alpine relics, also support this hypothesis. The polymorphism of *C. hypochaeridea* has probably resulted from its adaptation to altitudes lower than the altitudes of the alpine relics.

42. *Crepis chirindica* S. Moore

Jour. Bot. 54: 286. 1916. (Fig. 71.)

Perennial, about 5 dm high; caudex 1.5 mm wide at the leafy crown; caudical leaves up to 10 cm long, 1.5 cm wide, oblanceolate, obtuse, remotely shortly denticulate, sparsely pubescent on both sides, especially on midvein beneath; cauline leaves few, small, lance-linear or bractlike; stems erect, sulcate, or striate, glabrous, fistulose, at least toward summit, cymosely branched from near base, branches remote, elongated, 1-4-headed; peduncles 2.5-15 cm long, hispidulous with short black setae, somewhat thickened at summit, canescent-tomentose and finely gland-pubes-

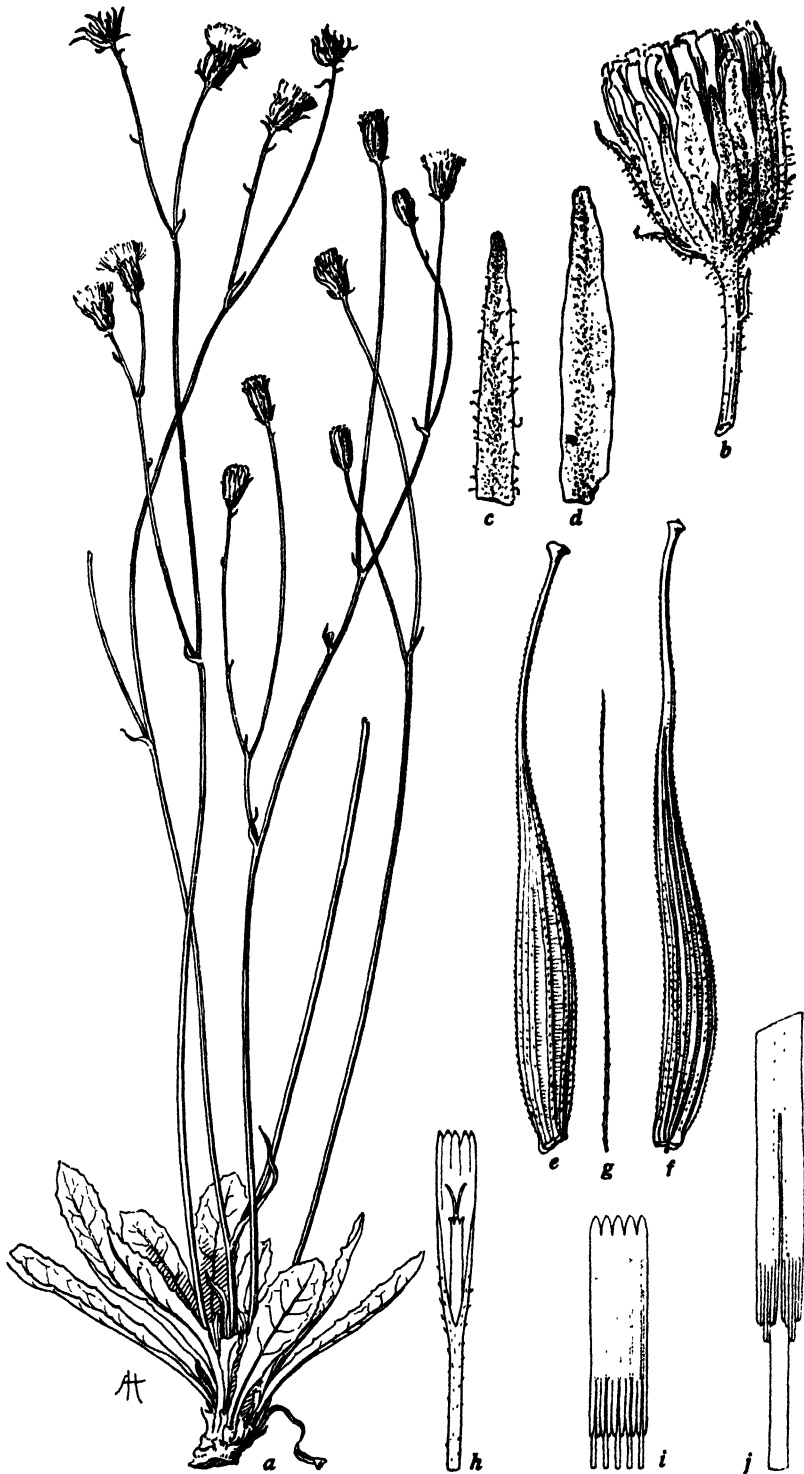


Fig. 71. *Crepis chirindica*, from type (BM): a, plant, $\times \frac{3}{8}$; b, flowering head, $\times 2$; c, d, 2 inner involucre bracts, outer face, $\times 4$; e-g, 2 achenes and a pappus seta, $\times 8$; h, floret lacking ovary, $\times 4$; i, anther tube, $\times 8$; j, detail of appendages, $\times 32$.

cent near the head; heads erect, rather large, many-flowered; involucre campanulate, 12 mm long, 8 mm wide in fruit, gland-pubescent with short pale hairs and brown glands, bearing occasional black setules, the bracts becoming lax but not reflexed at maturity; outer bracts 10, unequal, longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as inner bracts, linear, 0.6–0.8 mm wide; inner bracts 16, in 2 series, the outer ones a little shorter, linear, the inner ones lanceolate, membranous-margined, obtuse, all glabrous on inner face, little changed at maturity; receptacle areolate, naked (?); corolla 11 mm long; ligule 1.2 mm wide; teeth 0.2–0.5 mm long; corolla tube 4.5 mm long, slender, sparsely beset with very short blunt and longer (up to 0.25 mm) acicular hairs extending onto ligule; anther tube 4×0.9 mm dis.; appendages 1 mm long, oblong, acute; filaments 0.5 mm longer; style branches 1 mm long, 0.08 mm wide, yellow; achenes very dark brown, 9.5–10.5 mm long, 1 mm wide, gradually attenuate into a yellow beak 3 mm long and 0.15 mm wide, with pappus disk 0.3 mm wide, constricted above the prominent pale callosities surrounding the hollow base, 16-ribbed, ribs nearly equal, narrow, rounded, strongly spiculate, especially on the beak; pappus yellowish-white, 7.5 mm long, 3-seriate, the setae nearly equal in length and width, moderately coarse, firm but not brittle, very persistent. Flowers yellow.

Known only from the type specimen.

Monomorphic.

Rhodesia: Melsetter dist. (Gazaland), Mt. Chirinda, *Swynnerton* in 1913 (BM, UCf).

Relationship

Crepis chirindica is close to *C. hypochacridea*, especially subsp. *rhodesica*; but it is distinct from all 3 subspecies in the tall stature of the plant, the unequal inner bracts of the involucre, the long yellow-beaked achenes with more numerous ribs, the small style branches, and the long narrow anther appendages. It is less close to *C. Newii*, *C. simulans*, and *C. Swynnertonii*.

43. *Crepis congoensis* Babc.

Bull. Jard. Bot. Etat (Bruxelles) 15: 301. 1937. (Fig. 72.)

Perennial, 3.4 dm high; caudex 1 cm wide, woody, leafy at summit; caudical leaves up to 10.5 cm long, 1.8 cm wide, oblanceolate, acute, cuspidate, irregularly serrately dentate, attenuate into a winged petiole, hispidulous beneath, especially on midvein, glabrous above, midvein prominent; cauline leaves few, small, lance-linear, acuminate; stems 8 from a single caudex, terete, striate, shortly pubescent near base with glandless hairs, glabrous above, branched from near base, branches remote, elongated, flexuous, each branch bearing 1–4 heads in a corymbiform cyme; peduncles 4–13 cm long, gland-pubescent with short yellow hairs; heads erect, medium, many-flowered; involucre 10–11 mm long, 6–7 mm wide, cylindric-campanulate, fuscous-tomentose, and, like peduncle, gland-pubescent, completely reflexed at maturity; outer bracts 12–13, with 2–4 subtending ones, unequal, longest $\frac{1}{3}$ as long as inner bracts, lanceolate, obtuse, ciliate at apex; inner bracts 12–18, lanceolate, obtuse, innermost scarious-margined, becoming carinate and indurate but not spongy-thickened; receptacle alveolate, alveolae crater-form, surrounded with lacinate scales; corolla 10.5 mm long; ligule 1.25 mm wide; teeth 0.2–0.4 mm long; corolla tube 4.5 mm long, pubescent with short stout 2–6-celled simple or furcate tortuous hairs; anther tube 3.25×1 mm dis., very delicate, membranous, narrowed at base by union of the narrow appendages; appendages 0.7 mm long, lanceolate, acuminate; filaments 0.5 mm longer; style branches 1.25 mm long, 0.1 mm wide, attenuate, yellow, achenes dark reddish-brown, 7–8 mm long, fusi-

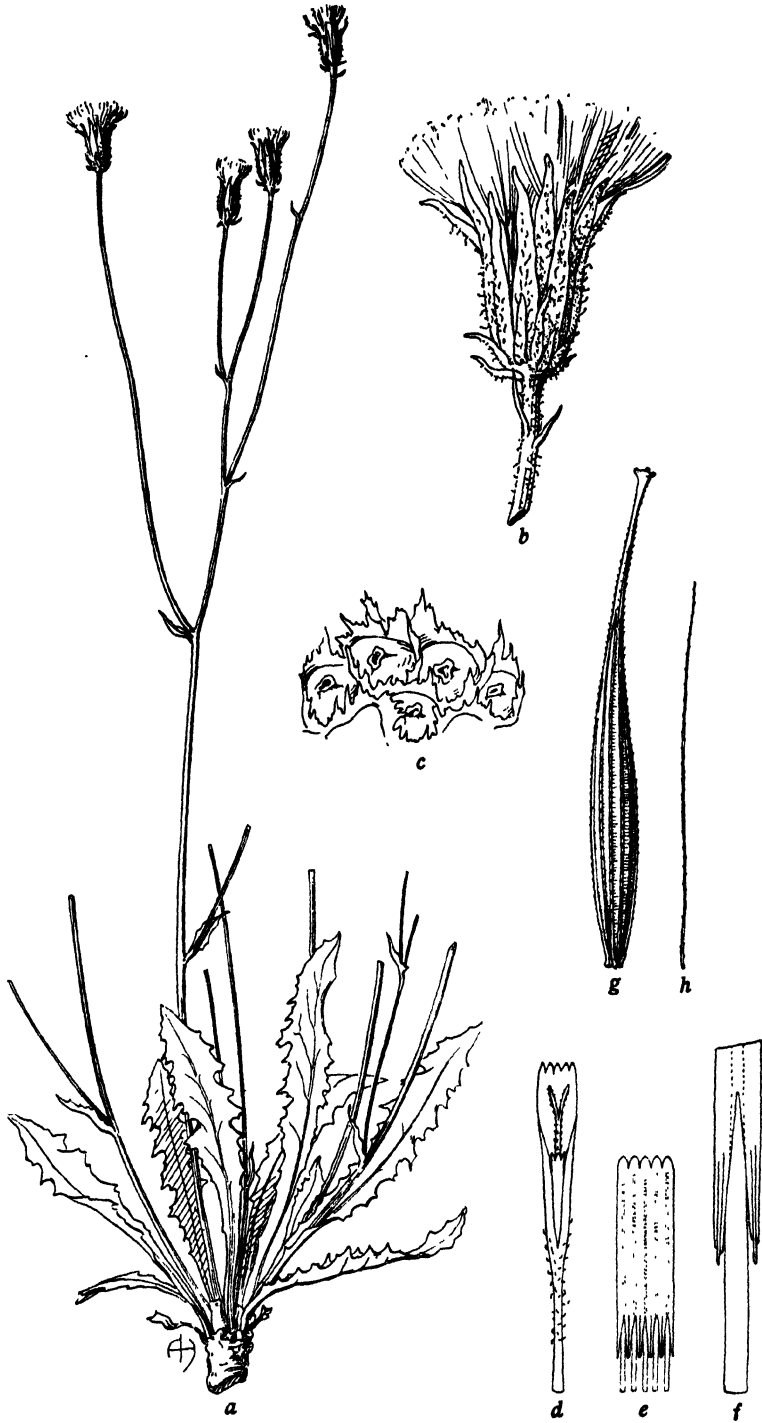


Fig. 72. *Crepis congoensis*, from type (K): a, plant, $\times \frac{1}{2}$; b, nearly mature head, $\times 2$; c, detail of receptacle, $\times 16$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, h, achene and a pappus seta, $\times 8$.

form, strongly attenuate into a beak shorter than or nearly equal to body, pale near summit, with slightly expanded pappus disk, constricted at the pale-calloused hollow base, 12–14-ribbed, ribs narrow, finely spiculate; pappus yellowish-white, 6 mm long, 2-seriate, rather fine, soft, persistent. Flowering Oct.; flowers yellow.

Known only from the type specimen which was collected in October, 1911.

Monomorphic.

Belgian Congo: Lubumbashi, about 12° S., 28° E., Elisabethville, 1450 m, *Rogers 10072* (K).

Relationship

Crepis congoensis is nearest to *C. Newii* from which it is very distinct in the strongly dentate leaves, the deeply alveolate receptacle, the narrower corolla and very different pubescence on the corolla tube, the shorter anther tube with narrower appendages, and the more finely beaked achenes.

44. *Crepis caudicalis* Babc.

Bull. Jard. Bot. Etat (Bruxelles) 15: 303. 1937. (Fig. 73.)

Perennial, 1–2.5 dm high; caudex vertical, 0.5–1 cm wide, prolonged into a tap-root, becoming branched and suffrutescent, covered with brown bases of old leaves, leafy at crown; stems 1–3, erect or ascending, slender, terete, finely striate, glabrescent, simple and 1-headed or 1–3-furcate and cymosely 2–4-headed; caudical leaves 2–4 cm long, 1–1.5 cm wide, obovate to oblanceolate, obtuse or acute, denticulate, corneous-mucronate, attenuate into a winged petiole equal to blade or much shorter, puberulous with short pale gland hairs, becoming glabrescent; lowest cauline leaves (near base) similar, the others very small, linear, sessile, denticulate, or ciliate at margin, uppermost bractlike; peduncles 2.5–6 cm long, slender, slightly broader and finely gland-pubescent at summit; heads erect, medium, 20–30-flowered; involucre campanulate, 8–10 mm high, 4 mm wide at middle in fruit, \pm pubescent with short pale gland hairs; outer bracts 7–8, unequal, longest $\frac{1}{2}$ – $\frac{2}{3}$ as long as inner bracts, linear, less than 1 mm wide, glabrescent; inner bracts 12–14, lanceolate, acute, rounded and white-ciliate at tip, glabrous on inner face, medio-dorsally nerved near base, becoming rounded-carinate and indurate but not spongy-thickened at base; receptacle alveolate; corolla 12 mm long; ligule 1.75 mm wide at middle, 1–1.25 mm at summit; teeth 0.25–0.4 mm long; corolla tube about 4 mm long, pubescent from base to summit with minute (up to 0.07 mm long) acicular hairs borne singly or in clumps; anther tube 3.5×1 mm dis.; appendages 0.6 mm long, obliquely acute, partly united; filaments 0.5 mm longer; style branches 1 mm long, 0.15 mm wide, obtuse, yellow; achenes light brown, 7.5–8 mm long, 0.5 mm wide, laterally subcompressed, very gradually attenuate upward into a coarse beak 0.15 mm wide below the pale summit, pappus disk 0.3 mm wide, constricted above the narrow oblique pale-calloused hollow base, 10-ribbed, ribs equal, narrow, rounded, finely spiculate nearly to the apex; pappus yellowish-white, 4–5 mm long, 2-seriate, nearly equal, rather fine, soft, persistent. Flowering Feb., Mar.; flowers yellow.

Monomorphic.

Cameroon: Pass Tchape, in the Pass, 1400 m, burned-over savanna with few trees and shrubs, *Ledermann 2819* (B, UCf) type; *ibid.*, 1420 m, recently burned savanna, *Ledermann 2745* (B).

Known only from the type locality. Pass Tchape is not given in Stieler's or The Times Atlas. The given altitude would restrict it to N. Cameroon, and "Pass" suggests mountainous country, probably the Cameroon Mts.



Fig. 73. *Crepis caudicalis*, from type (B): *a*, *b*, plants, $\times 1$; *c*, young head, $\times 2$; *d*, floret lacking ovary, $\times 2$; *d'*, detail of ligule teeth, $\times 50$; *e*, anther tube, $\times 8$; *f*, detail of appendages, $\times 32$; *g*, fruiting head, $\times 2$; *h*, adjacent inner involucral bracts, $\times 4$; *i*-*k*, 2 achenes and a pappus seta, $\times 8$.

Relationship

Crepis caudicalis is related to *C. Newii* and *C. simulans*, from both of which it is distinct in the suffruticulose caudex, the strongly attenuate ligules, and the very narrow, light brown achenes. It is less close to *C. scaposa* and its allies of E. Africa, although superficially somewhat similar.

45. *Crepis Newii* Oliv. et Hiern

Fl. Trop. Afr. 3: 449. 1897. (Figs. 74–78.)

Perennial, 1–5 dm high; root vertical, tapering or subnapiform, woody; caudex short, simple or few-divided, 0.5–1.5 mm wide, leafy; caudical leaves numerous, 2–16 cm long, 1–4 cm wide, oblanceolate or elliptic, acute or obtuse, cuspidate or mucronate at apex, sinuately denticulate to acutely dentate with recurved teeth, attenuate into the short winged petiole with broader clasping base, hispidulous, pubescent, puberulous or glabrous; cauline leaves small, linear, denticulate or entire or bractlike; stems 1–4, erect or ascending, terete, pithy, striate, glabrous, puberulous, tomentulose at the bifurcations, or sparsely hispidulous, remotely cymosely 2–4-branched, first branch sometimes from near base, lower branches erect, elongated, cymosely few-headed; peduncles 1–13 cm long, erect, slender, bracteate; heads erect, medium, 25–50-flowered; involucre cylindric-campanulate in fruiting heads, 9–11 (12) mm long, 5–7 mm wide at middle, sparsely hispidulous with black glandless hairs on inner bracts, or finely pubescent with short pale gland hairs and sometimes with longer or darker setules intermixed, or rarely not pubescent but canescent-tomentulose; outer bracts 7–15, with 1–6 subtending ones; always less than 1 mm wide, $\frac{1}{3}$ – $\frac{1}{2}$ as long as inner bracts; inner bracts 12–15, lanceolate, obtuse, finely ciliate at apex, glabrous on inner face, becoming carinate dorsally and more or less but not conspicuously spongy-thickened at base in mature heads; receptacle alveolate or areolate-fimbriate, fimbriae low, naked or shortly ciliate; corolla 10–15 mm long; ligule 1–2 mm wide; teeth 0.15–0.9 mm long; corolla tube 3–5.5 mm long, pubescent with minute papilliform and acicular hairs; anther tube (3.25)4.25 \times 1 (1.25) mm dis.; appendages 0.5–0.8 mm long, oblong; filaments unequal or equal, extending beyond appendages 0.6–1.25 mm; style branches 0.7–1.5 mm long, yellow; achenes reddish-brown (in subsp. *Greenwayi*, deep purplish), 4–7.5 mm long, attenuate to the narrow apex or shortly and coarsely beaked, narrowed at the pale-calloused hollow base, 10–15-ribbed, ribs rounded, muriculate or finely spiculate; pappus yellowish or whitish, 4.5–7 mm long, 2-seriate (in subsp. *Greenwayi*, 1-seriate), persistent. Corolla, anther tube, and style branches yellow.

Tropical Africa from the eastern escarpment region to middle Angola, middle E. Cameroon and S.E. Nigeria, mostly in grasslands from about 1000 to 2300 m alt.

This polymorphic species comprises a number of local populations which differ sufficiently from one another to require their recognition here as subspecies. Collections have been too meager and widely separated thus far to throw much light on continuity of distribution or on overlapping and intergrading of these subspecies. Two forms are known, however, which appear to be intergrades (see m.v. 1 and 3).

Key to the Subspecies of Crepis Newii

Caudical leaves hispidulous on both sides with yellow glandless setules; involucre hispidulous with black glandless hairs, or canescent-tomentulose; root tapering from the broader, often divided caudex.

Plant 2.5–5 dm high; outer involucre bracts 9–10, the widest 0.5–0.8 mm wide at base; achenes reddish-brown, 4.5–7.5 mm long; pappus 6–7 mm long, 2-seriate 45, *a. typica*, p. 370

Plant 1–2 dm high; outer involucre bracts 12–15, the widest 0.5 mm or less wide at base; achenes dark purplish, 4–5 mm long; pappus 5 mm long, 1-seriate 45, *b. Greenwayi*, p. 372

Caudical leaves glabrous, puberulent, or very finely pubescent; involucre finely pubescent with short pale gland hairs and sometimes with longer or darker setules intermixed; root sub-napiform, constricted below the usually simple caudex.

Plant 4–5 dm high; leaves glabrous or puberulous, not brown-woolly at base; corolla in marginal florets 11–13 mm long.

Outer involucre bracts 7–9, with 1 or 2 subtending ones, neither strongly carinate nor pale-scarious; setae on inner bracts black.

Caudical leaves 5–7 cm long, 1–1.8 cm wide; corolla about 13 mm long; anther tube about 4.25 mm long; achenes 5–6.5 mm long; pappus 4.5 mm long, but in m.v. 1, 5–6 mm long 45, *c. bumbensis*, p. 374

Caudical leaves 6–16 cm long, 1.5–4 cm wide; corolla about 11 mm long; anther tube about 3.5 mm long; achenes 7 mm long; pappus 6 mm long 45, *d. kundensis*, p. 374

Outer involucre bracts 9–11, with 3–6 subtending ones, strongly carinate and pale-scarious; setae on inner bracts yellow 45, *e. nyasensis*, p. 374

Plant 1–3 dm high; leaves finely pubescent on both sides and brown-woolly at base; corolla about 10 mm long; achenes 6.5–7.5 mm long; pappus 5 mm long 45, *f. itakensis*, p. 375

45, *a. Crepis Newii typica* subsp. nov. Planta 2.5–5 dm alta; radix obconica non napiformis; folia caudicalia hispidulosa; involucrea hispidulosa vel tomentulosa, squamis exterioribus 9–10 ad basim 0.5–0.8 mm latis, interioribus 12–15 lanceolatis obtusis; corolla 11–15 mm longa; antherae circa 4 mm longae; achaenia fusca 4.5–7.5 mm longa; pappus 6–7 mm longus biseriatus.

Plant 2.5–5 dm high; caudical leaves acute, cuspidate, or obtuse, mucronate, dentate with recurved teeth, or denticulate; stems 1–4 to each caudex; peduncles \pm hispidulous with fine short black glandless hairs; outer involucre bracts 9–10, the widest 0.5–0.8 mm wide at base, sometimes hispidulous, like inner bracts, with black glandless hairs; corolla 11–15 mm long; corolla tube 3–5.5 mm long, beset with papilliform and acicular hairs 0.05–1 mm long; anther tube (3.75) 4.25 \times 1 mm dis.; appendages 0.75 mm long, oblong, acute or truncate; filaments unequal, 0.6–1.25 mm longer; style branches 1–1.5 mm long, 0.15 mm wide; achenes reddish-brown when fully mature, orange when partly mature, 4.5–7.5 mm long, about 0.75 mm wide, moderately or strongly attenuate upward or sometimes shortly and coarsely beaked, with yellowish expanded pappus disk, narrowed near the yellow-calloused hollow base, about 15-ribbed, ribs rounded; pappus pale yellow, 6–7 mm long, 2-seriate, moderately coarse, stiff. Flowering July–Nov. See fig. 74.

Hieraciodes Newii O. Kuntze, Gen. 1: 346. 1891.

Tanganyika Terr.: “around Kilimanjaro,” Mr. and Mrs. New (K) type; S.W. Arusha Prov., Mbulu dist., near Ndareda, about 1500 m, *Haarer 1823* (K, Amani) m.v. 1; Iringa Prov., E. Mufindi, about 1800 m, *Haarer 1611* (K); Iringa Prov., Dabaga, 1900 m, on recently cultivated land, very sandy, pale yellow soil, *Greenway 3401* (UC). The fragmentary specimens in Herb. Berol., cited by Fries (355), have not been seen by me. If they are of this subspecies, they provide two other localities south and southwest of Kilimanjaro, one of which is Mt. Gurui in Kondo Prov.

Minor Variant of C. Newii typica

1. Caudical leaves obtuse and denticulate; involucre sparsely tomentulose, not hispidulous. In the features just noted, this form approaches subsp. *Greenwayi*; but the plants are tall, and floret and achene characters are as in subsp. *typica*. *Haarer 1823* (K, Amani), about 1500 m, near Ndareda, Mbulu dist., S.W. Arusha Prov., Tanganyika Terr.

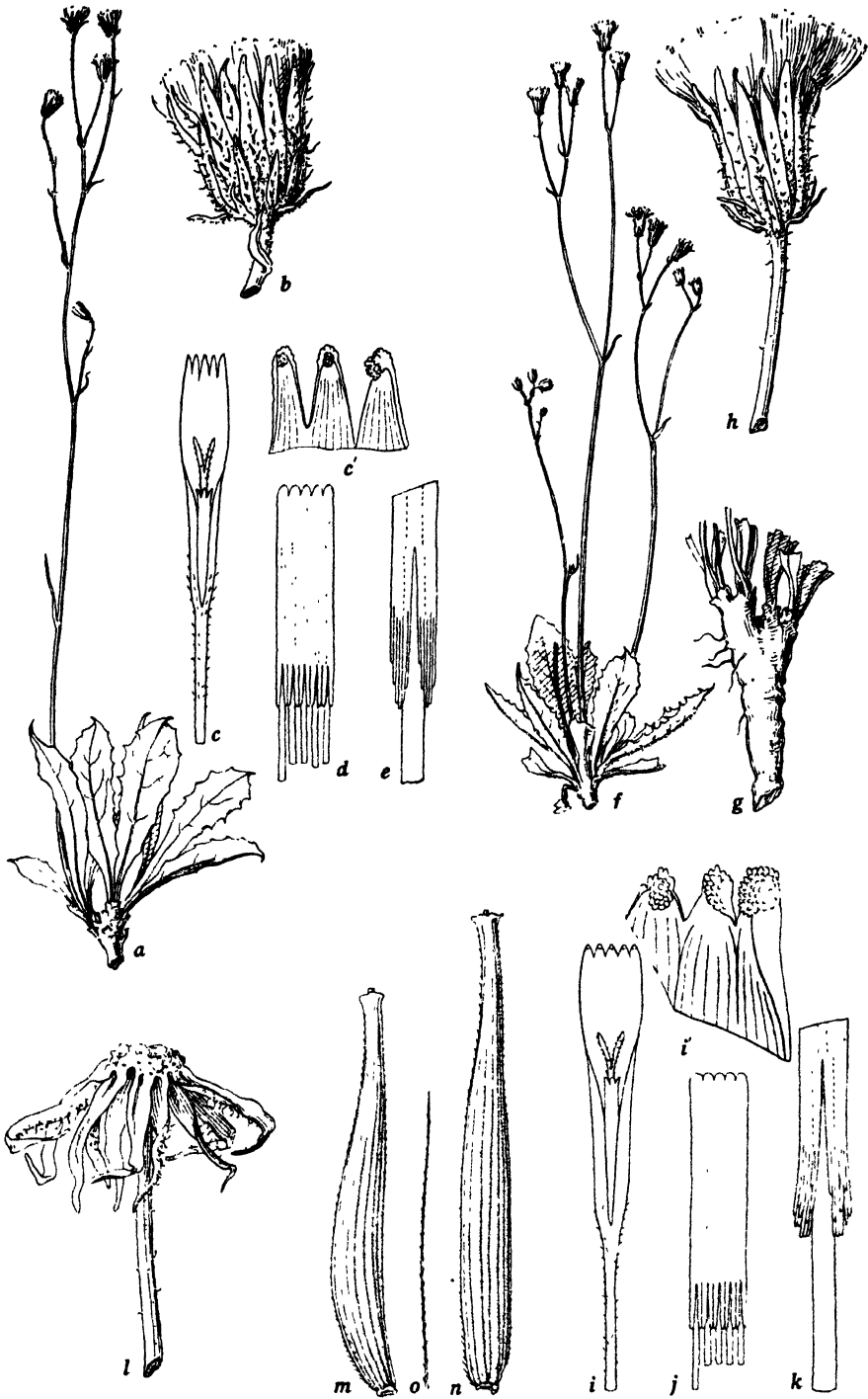


Fig. 74. *Crepis Newii typica*, a-e, from type (K); f-o, from Greenway 3401 (UC 513277): a, plant, $\times \frac{1}{4}$; b, head, $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule teeth, $\times 25$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, plant, $\times \frac{1}{4}$; g, caudex and base of caudical leaves (reduced); h, fruiting head, $\times \frac{1}{4}$; i, floret lacking ovary, $\times 4$; i', detail of ligule teeth, $\times 25$; j, anther tube, $\times 8$; k, detail of appendages, $\times 32$; l, old head, $\times 2$; m-o, 2 achenes and pappus seta, $\times 8$.

45, *b. Crepis Newii Greenwayi* subsp. nov. Planta 1–2 dm alta; folia caudicalia obtusissima mucronata denticulata; involucria 9–10 mm longa 4–5 mm lata, squamis exterioribus 12–15 circa 0.5 mm latis glabris, interioribus tomentulosis; corolla circa 10 mm longa, tubo 3 mm longo pubescenti; antherae 3.5 mm longae; achaenia nigrofusca 4–5 mm longa fusiformia erostrata 10–12-costata; pappus albus vel flavidus 5 mm longus.

Plant 1–2 (in cult. 3) dm high; caudex 1-stemmed; caudical leaves very obtuse, mucronate, denticulate; peduncles canescent-tomentulose; involucries 9–10 mm long,

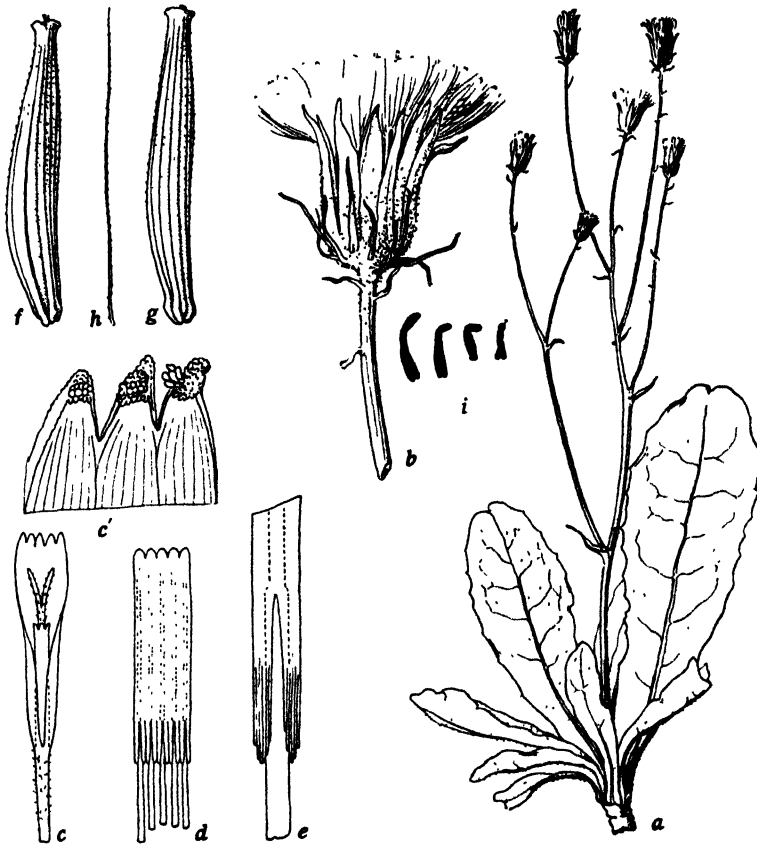


Fig. 75. *Crepis Newii Greenwayi*, from type (UC 513276): *a*, plant, $\times \frac{1}{2}$; *b*, fruiting head, $\times 2$; *c*, floret lacking ovary, $\times 4$; *c'*, detail of ligule teeth, $\times 25$; *d*, anther tube, $\times 8$; *e*, detail of appendages, $\times 32$; *f-h*, 2 achenes and pappus seta, $\times 8$; *i*, somatic chromosomes of seedlings grown from type collection (hort. genet. Calif. 3274), $n = 4$, $\times 1250$.

4–5 mm wide at middle; outer involucrial bracts 12–15, the widest 0.5 mm or less wide at base, glabrous; inner bracts canescent-tomentulose; corolla about 10 mm long; corolla tube 3 mm long, sparsely beset with minute papilliform hairs 0.05 mm long; anther tube 3.5×1 mm dis.; appendages 0.6–0.8 mm long, oblong, acute; filaments unequal, 1–1.25 mm longer; style branches 1.4 mm long, 0.15 mm wide; achenes deep purplish-brown, 4–5 mm long, 0.7–0.8 mm wide, with a narrow white ring at both pappus disk and base, fusiform, definitely attenuate to summit, constricted at the narrow hollow base, 10–12-ribbed, ribs nearly equal, rather strong, rounded; pappus white or yellowish, 5 mm long, 1-seriate, rather fine, soft. Flowering Aug.–Nov. Chromosomes, $2n = 8$. See fig. 75.

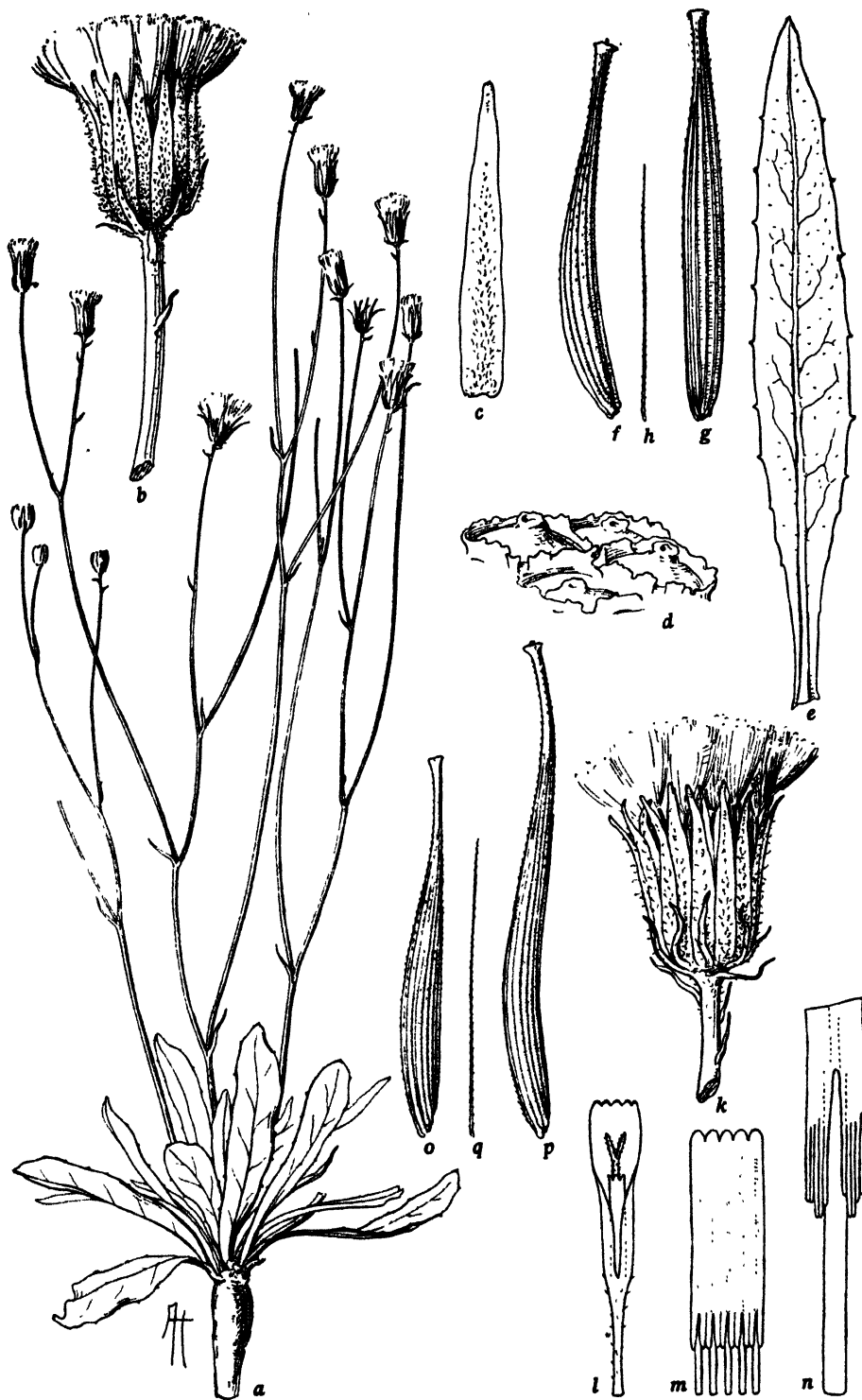


Fig. 76. *Crepis Newii*, a-h, subsp. *bumbensis*, from type (BM); k-q, subsp. *itakensis*, from type (UC 513249): a, plant, $\times \frac{1}{2}$; b, head, $\times 2$; c, inner involucre bract, outer face, $\times 4$; d, detail of receptacle, $\times 25$; e, basal cauline leaf, $\times 2$; f-h, 2 achenes and a pappus seta, $\times 8$; k, head, $\times 2$; l, floret lacking ovary, $\times 4$; m, anther tube, $\times 8$; n, detail of appendages, $\times 32$; o-q, 2 achenes and a pappus seta, $\times 8$.

Tanganyika Terr.: Iringa Prov., Msima Stock Farm, grassland, 1636 m, *P. J. Greenway 3529B*, (UC 513276, Amani) type, isotype; Iringa Prov., Njombe (west of Msima Stock Farm), *Lynes D49* (K) m.v. 2. Cultivated specimens grown in a greenhouse at Berkeley from seed taken from the type material have faithfully reproduced the distinguishing features of this subspecies.

Minor Variant of C. Newii Greenwayi

2. A reduced form, due, perhaps, to drought or competition. Plant 1–1.5 dm high; caudical leaves 2.5–3.5 cm long; stem slender, 1–2-headed, but with 3–5 abortive heads borne racemously; heads rather small; involucre 6–7 mm high. Floral characters typical; corolla about 10 mm long; anther tube about 3 mm long; style branches 1.25 mm long; pappus yellowish-white, 5 mm long; achenes lacking. *Lynes D49* (K) Njombe, Iringa Prov., Tanganyika Terr.

45, *c. Crepis Newii bumbensis* (Hiern) comb. nov. Plant about 4 dm high; caudical leaves 5–7 cm long, 1–1.8 cm wide, puberulous on lower face with minute gland hairs or spreading glandless hairs; involucre 10–11 mm long; inner involucre bracts gland-pubescent with very short pale hairs and slightly longer black setae scattered from base to apex, \pm thickened at base in fruit; corolla about 13 mm long; anther tube about 4.25×1 mm dis.; achenes 5–6.5 mm long, shortly and coarsely beaked; pappus 4.5 mm long. See fig. 76, *a–h*.

Crepis bumbensis Hiern, Cat. Welw. Afr. Pl. 3: 616. 1898.

Crepis bumbensis typica Babc., Bull. Jard. Bot. Etat (Bruxelles), 15: 298. 1937.

The type locality is given by Hiern as Bumbo, in the wooded meadows of Catumba, with the observation, "rather rare; flowers and fruits, Dec., 1859."

Angola: Benguela, Bumbo dist., *Welwitsch 3667* (BM, UCf, K) type, isotype; Loanda, Malange dist., *Gossweiler* in 1903 (P) m.v. 3; Malange *Gossweiler* (K) m.v. 3.

Minor Variant of C. Newii bumbensis

3. Very robust; plant 7.5 dm high; leaves broader and petioles narrower than in typical subsp. *bumbensis*; stems unbranched for $\frac{2}{3}$ of their length; aggregate inflorescence corymbiform; involucre bracts lacking gland setules; pappus 5–6 mm long. *Gossweiler* in 1903 (P, K) Malange dist., Loanda, Angola.

45, *d. Crepis Newii kundensis* (Babc.) comb. nov. Plant 4–5 dm high; caudical leaves 6–16 cm long, 1.5–4 cm wide, puberulous, especially on veins, or glabrescent; involucre 9–10 mm long; inner involucre bracts gland-pubescent and black-setose toward apex, the setae short and broad based, becoming strongly carinate and pale spongy-thickened at base at full maturity; corolla about 11 mm long; ligule 1.5 mm wide; teeth 0.25–0.3 mm long, obtuse; corolla tube pubescent from base to summit, as on lower part of ligule, with stout papilliform and acicular hairs 0.05 mm long disposed singly or in groups; anther tube 3.5×1 mm dis.; appendages 0.6 mm long, oblong, acute; filaments 0.75 mm longer; style branches 1.25 mm long, 0.1 mm wide; achenes about 7 mm long, coarsely beaked, ribbed to summit; pappus 6 mm long. See fig. 77.

Crepis bumbensis kundensis Babc., Bull. Jard. Bot. Etat (Bruxelles), 15: 300. 1937.

Cameroon and S.E. Nigeria, in grasslands of the middle altitudes.

Cameroon: savannas of the lower highlands, about 6° N., 14° E., near Kunde, Kisare, *Mildbraed 9214* (B) type, in fruit in Feb. (?) or May (?). **S.E. Nigeria:** Bamenda, Rambuluc, *Thorbecke 241* (B).

45, *e. Crepis Newii nyasensis* subsp. nov. Planta 6–7.5 dm alta; folia caudicalia 10–15 cm longa 2–3 cm lata glabra; involucre 9–10 mm longa 4–5 mm lata, squamis exterioribus numerosis carinatis ad basim spongioso-incrassatis pallidis scariosis, interioribus glanduloso-pubescentibus et setulosis intermixtis; corolla 11–13 mm

longa, ligula 8–10 mm longa 1.25 mm lata, tubo pubescenti; antherae circa 4 mm longae; achenia circa 5 mm longa; pappus 6–7 mm longus.

Plant 6–7.5 dm high; caudical leaves 10–15 cm long, 2–3 cm wide, glabrous on both sides; involucre 9–10 mm long, 4–5 mm wide at middle; outer bracts 9–11, with 5–6 subtending ones, strongly carinate, thickened at base, pale-scarious; inner bracts gland-pubescent with short yellow hairs and stronger yellow or greenish setules, becoming carinate, spongy-thickened at base in fruit; corolla 11–13 mm long; ligule 1–1.25 mm wide; teeth 0.25–0.5 mm long; corolla tube 3–3.5 mm long, pubescent with papilliform and acicular hairs up to 0.12 mm long; anther tube (3.75) 4.25 × 1 mm dis.; appendages 0.5–0.6 mm long, oblong, sagittate; filaments 1.25 mm longer; style branches 1–1.2 mm long, 0.15 mm wide; achenes about 5 mm long, strongly attenuate upward, not beaked; pappus 6–7 mm long. See fig. 78.

Known only from the type locality.

S. Tanganyika Terr.: Kymbila dist., north of Lake Nyasa, *Stolz 396* (Brussel, Amani) type, isotype.

45, f. *Crepis Newii itakensis* (Babc.) comb. nov. Plant 1–3 dm high; caudical leaves 2–8 cm long, 1–2 cm wide, densely pubescent on both sides with erect setiform yellow glandless hairs, brown-woolly at base of petiole; involucre 10–12 mm long; inner involucre bracts gland-pubescent with short yellowish hairs bearing brown glands, not setose, becoming carinate and thickened at base in fruit; corolla 10 mm long; ligule 1.75 mm wide; teeth 0.15–0.2 mm long, obtuse; corolla tube about 4 mm long, sparsely covered with papilliform and acicular hairs up to 0.2 mm long disposed singly or in groups; anther tube 3.75 × 1.25 mm dis.; appendages 0.6 mm long, oblong, acute; filaments 0.75 mm longer; style branches 0.7–0.9 mm long, 0.15 mm wide, acute; achenes 6.5–7.5 mm long, gradually attenuate into the short pale smooth beak; pappus 5 mm long. See fig. 76, k–q.

Crepis bumbensis itakensis Babc., Bull. Jard. Bot. Etat (Bruxelles), 15: 299. 1937.

Known only from the type locality, where it was collected Sept. 1, 1933.

S.W. Tanganyika Terr.: Iringa Prov., Rungwe reg., northwest of Lake Nyasa, Itaka, grazed areas in *Hyparrhenia-Themeda* grassland subject to fires, 1515 m, *Greenway 3655* (UC 513249) type.

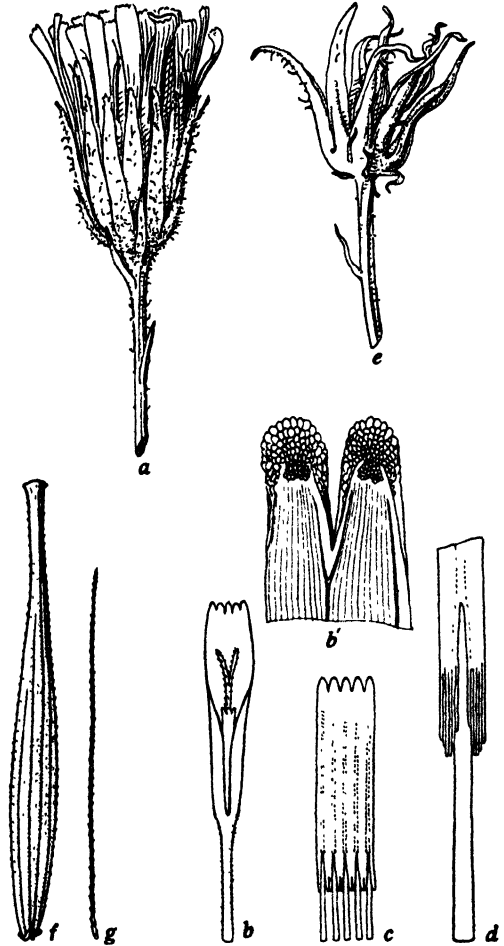


Fig. 77. *Crepis Newii kundensis*. a–d, from Thorbeck 241 (B); e–g, from type (B): a, flowering head, × 2; b, floret lacking ovary, × 4; b', detail of ligule teeth, × 50; c, anther tube, × 8; d, detail of appendages, × 32; e, old fruiting head, × 2; f, g, achene and a pappus seta, × 8.

Relationship

Crepis Newii is most nearly related to *C. simulans* and *C. caudicalis*, from both of which it is distinct in having the inner involucre bracts spongy-thickened at maturity. From *C. simulans* it also differs in the longer style branches and in the pubescence of the caudical leaves, which may be setulose but not glandulose. From *C. caudicalis* it differs in the simple or few-divided caudex, in the usually more numerous outer involucre bracts, in the longer caudical leaves, and in the dark colored, wider achenes.

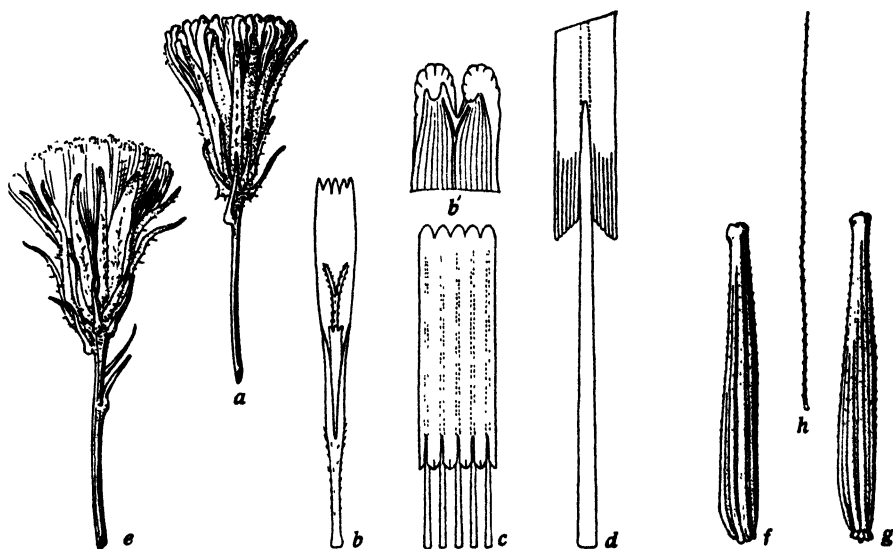


Fig. 78. *Crepis Newii nyasensis*, from type (Brussel): *a*, flowering head, $\times 2$; *b*, floret lacking ovary, $\times 4$; *b'*, detail of ligule teeth, $\times 50$; *c*, anther tube, $\times 8$; *d*, detail of appendages, $\times 32$; *e*, fruiting head, $\times 2$; *f-h*, 2 achenes and a pappus seta, $\times 8$.

46. *Crepis scaposa* R. E. Fr.

Svensk Bot. Tidskr. 22: 360. 1928. (Figs. 79-82.)

Perennial, 0.3-3.5 dm high; root strong, woody, vertical; caudex 0.5-2 cm long, 0.5-2 cm wide, simple or divided, bearing scars or bases of old leaves, leafy at crown; caudical leaves numerous, oblanceolate, obtuse or acute, apiculate to minutely mucronate, finely denticulate to runcinate-pinnatifid, attenuate into a winged petiole, glabrous or with a few short scattered yellow glandless hairs; cauline leaves mostly bractlike or absent, occasionally 4-6 cm long, linear; stems 1-5, scapiform, 1-2-headed, terete, fistulose, striate, glabrous or puberulous below, canescent-tomentose to yellowish tomentose near head; heads erect, many-flowered; involucre 7-13 mm long, campanulate, bracts numerous, \pm imbricate, and with several subtending paler bracts, inner bracts \pm appressed-pubescent on inner face, becoming indurate, not or only rarely somewhat spongy-thickened at base when fully mature; corolla yellow, 8-15 mm long; anther tube yellow, 2-4 mm long; style branches yellow, 0.5-1.75 mm long; achenes brown, 4-7.5 mm long, subterete or subcompressed, fusiform, \pm attenuate upward or indefinitely and shortly beaked, constricted at the pale-calloused hollow base, 14-18-ribbed, ribs fine, nearly equal, very finely spiculate or muriculate; pappus white or yellowish, 5-6 mm long, 2-3-seriate, rather fine, soft, persistent.

E. tropical Africa in S.W. Kenya and N.E. Tanganyika, mountains and plateaus; and in N. Kiwu Prov. of E. Belgian Congo.

The polymorphic nature of this species was recognized by Fries (*loc. cit.*), and the present treatment is essentially similar to his except for the recognition of one additional subspecific entity (cf. subsp. *eximia*). All 4 subspecies are highly variable in vegetative characters, such as size of plant and length of flower stems. There is also considerable variation in the flowers and fruits within the subspecies, especially in the two more widely distributed ones, subsp. *afromontana* and *taraxaciformis*. Although the last-mentioned subspecies, in its typical forms, is definitely set apart from the rest of the species morphologically, yet certain of its variant forms so nearly approach some one of the other three subspecies that, for the present, its recognition as a species does not seem warranted.

The 4 subspecies, although not restricted to definite geographic areas, are fairly well separated altitudinally. There is more or less overlapping, however. Two of them, subsp. *typica* and *eximia*, are found at lower elevations in mountains and on grassy plains and steppes; and these two have been collected together at 2 stations. Yet they appear to differ morphologically to a degree sufficient to warrant their recognition as different entities. The other two subspecies occur at higher elevations and differ from each other in their associations.

Key to the Subspecies of Crepis scaposa

Inner involucrel bracts 12–16 or 18, in 1–2 series; usually \pm pubescent.

Inner involucrel bracts pale, nearly glabrous or with extremely short scattered black hairs; stems 0.15–0.9 dm high, 1-headed; plants of lower montane and plateau regions 46, *a. typica*

Inner involucrel bracts dark, pubescent or setulose, with black gland hairs or setules; stems 0.9–3.5 dm high (rarely less than 0.9 dm in reduced forms), 1–2-headed.

Corolla in marginal florets 9–11 mm long; caudical leaves mostly rounded-obtuse, the broadest 13–17 mm wide; plants of lower montane and plateau regions 46, *b. eximia*

Corolla in marginal florets 11–15 mm long; caudical leaves mostly acute or definitely apiculate, the broadest 5–13 (rarely 15) mm wide; montane plants, mostly of higher elevations 46, *c. afromontana*

Inner involucrel bracts 16–40, in 3–5 series, glabrous, often pale in midregion and with very dark margins; montane plants of upper bamboo regions and similar elevations 46, *d. taraxaciformis*

46, *a. Crepis scaposa typica* subsp. nov. Planta parva humilis; caulis monocephalus; folia breviter petiolata; involucreum 7–9 mm longum, squamis exterioribus 10 lanceolatis obtusis glabris pallidis, interioribus 12–18, lanceolatis obtusis pallidis biseriatis; corolla 9 mm longa; antherae 2.5 mm longae; achaenia immatura fulva 3 mm longa fusiformia.

Plant small and low; the densely leafy rosettes 4–8 cm wide; stems 0.1–0.9 dm high, 1-headed; caudical leaves up to 4.5 cm long, 1 cm wide, acute, very shortly petioled; involucre 7–9 mm high, 5–6 mm wide at middle; outer bracts about 10, unequal, $\frac{1}{2}$ – $\frac{2}{3}$ as long as inner bracts, 1 mm wide at base, lanceolate, obtuse, glabrous, pale; inner bracts about 14 in 2 nearly equal series, lanceolate, obtuse, entirely pale or darker at tip, ventrally appressed-pubescent, dorsally glabrous or dotted with very short fine black hairs; corolla 9 mm long; ligule 1.4 mm wide, pubescent dorsally near base with coarse several-celled acicular hairs up to 0.6 mm long; teeth 0.1–0.2 mm long, slightly crested, convex-capitate; corolla tube 3 mm long, glabrous, except for a few short acicular hairs near base of ligule; anther tube

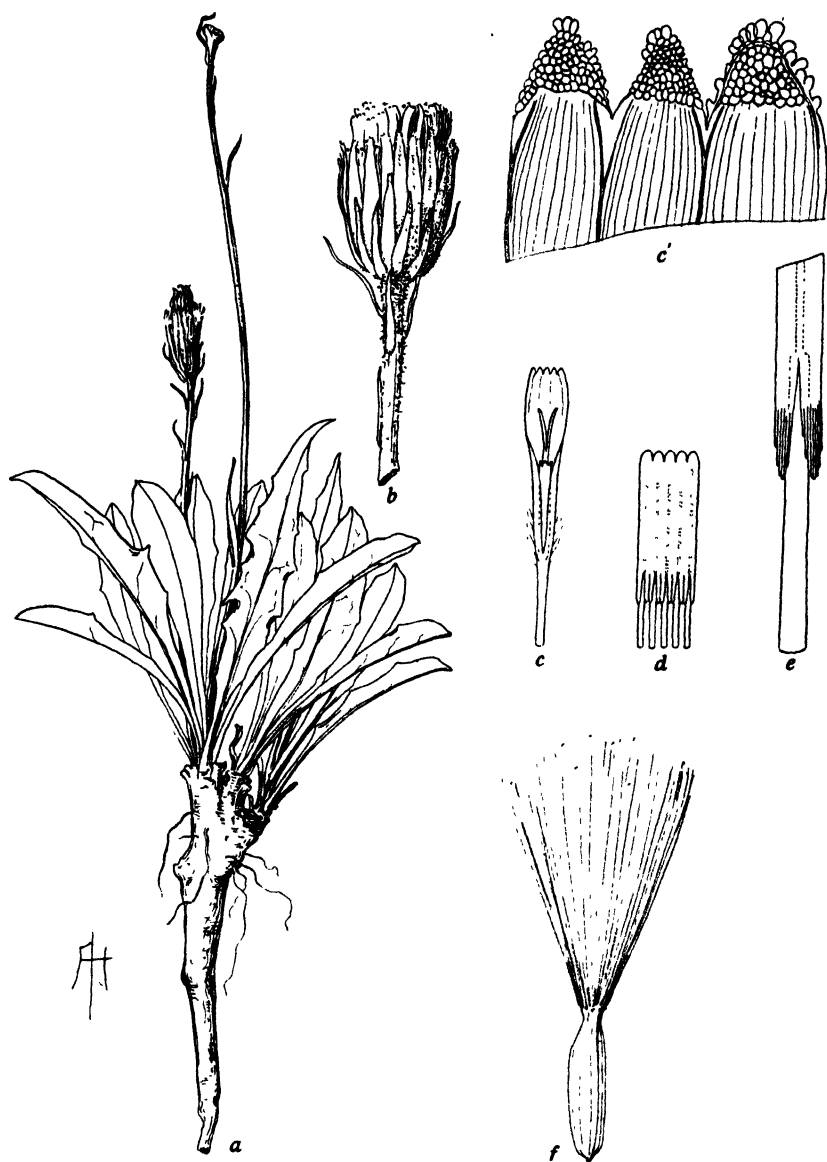


Fig. 79. *Crepis scaposa typica*, from type (Upsala): *a*, plant, $\times 1$; *b*, peduncle and head, $\times 2$; *c*, floret lacking ovary, $\times 4$; *c'*, detail of ligule teeth, $\times 50$; *d*, anther tube, $\times 8$; *e*, detail of appendages, $\times 32$; *f*, immature achene and pappus, $\times 8$.

about 2.5×1 mm dis.; appendages 0.5 mm long, oblong, acute; filaments 0.6–0.7 mm longer; style branches 1.2 mm long, 0.1 mm wide, acute; mature achenes lacking, immature achenes brown, 3 mm long, fusiform, constricted at summit, striate; pappus yellowish-white, about 5 mm long. Flowering Jan.–Mar. See fig. 79; and cf. Fries, *op. cit.*, Pl. VI, f. 2, *not* f. 3.

Local on Mt. Kenya, Mt. Aberdare, Mt. Kilimanjaro, and in N. Tanganyika.

Kenya: Mt. Kenya, E. side, at Churi, grassy place, *Fries 1837* (Upsala) type; Mt. Kenya, W. side, at Forest Station, grassy field, 2300 m, *Fries 825a* (Upsala); Mt. Aberdare, Kinangop

plateau, W. base of mountain, 2000 m, *Fries 2504* (Upsala). **Tanganyika:** Nanyuk-Meru, Marania R. dist., 2424 m, *van Someren 1740* (K); Kilimanjaro, Fan, Mashami, about 1500 m, *Haarer 1031a, b* (Amani).

46, *b. Crepis scaposa eximia* subsp. nov. Planta plerumque magis quam in subsp. *typica*, rosetta 0.9–1.8 dm lata; caules 0.9–3.5 dm alti; folia caudicalia ad 10 cm longa 1.7 cm lata obtusissima in petiolum longum attenuata; involucrem 9–12 mm longum 6–8 mm latum, squamis exterioribus 7–8 inaequalibus 4–7 mm longis circa 1 mm latis glabris pallidis, interioribus 14–16 biseriatis lanceolatis obtusis tenebricis \pm tomentulosis glanduloso-pubescentibus in facies interioribus glabris vel \pm pubescentibus; corolla 10–11 mm longa flava, ligula 6.5–7 mm longa 1–1.25 mm lata glabra vel ad basim pubescenti; antherae 2.75 mm longae flavae, appendicibus inaequalibus 0.4–0.6 mm longis acutis; rami styli 1–1.75 mm longi flavi; achania 4–6 mm longa 0.6–0.75 mm lata 18-costata; pappus 5–5.5 mm longus.

Plant usually larger and taller than in subsp. *typica*; rosettes 0.9–1.8 dm wide; stems 0.9–3.5 dm high, 1–2-headed; caudical leaves up to 10 cm long, 1.7 cm wide, rounded-obtuse, petiole $\frac{1}{5}$ – $\frac{1}{2}$ as long as whole leaf; involucre 9–12 mm long, 6–8 mm wide at middle; outer bracts 7–8, unequal, $\frac{1}{2}$ – $\frac{2}{3}$ as long as inner bracts, 1 mm wide at base, lanceolate, obtuse, glabrous, pale; inner bracts 14–16, in 2 nearly equal series, lanceolate, obtuse, dark with pale margins, ventrally glabrous or with a few appressed hairs, dorsally pubescent with black or brown gland hairs and \pm tomentulose; corolla 10–11 mm long; ligule 1–1.25 mm wide, glabrous, or with a few short acicular hairs near base; teeth 0.1–0.25 mm long, conspicuously crested, convex-capitate; corolla tube 3.5–4 mm long, sparsely beset with papilliform hairs 0.05–0.1 mm long and sometimes with acicular hairs near summit; anther tube 2.75×0.9 mm dis.; appendages unequal on same anther tube, 0.4–0.6 mm long, oblong, acute; filaments relatively long, extending beyond appendages more than 1 mm, the points of insertion of anthers unequal, sometimes as far apart as the length of the appendages; style branches 1–1.75 mm long, 0.1 mm wide; achenes dark brown, 4–6 mm long, 0.6–0.75 mm wide, 18-ribbed; pappus 5–5.5 mm long. Flowering Dec.–Feb. See fig. 80; and cf. *Fries, loc. cit.*, Pl. VII, f. 1.

Local in S. Kenya and N. Tanganyika.

Kenya: Mt. Kenya, W. side, near Forest Station, 2300 m, *Fries 524* (Upsala) type; *ibid.*, *Fries 825b* (Upsala); Limuru Station, grassland, 2121 m, *Dümmer 1681* (K) m.v. 2. **Tanganyika:** Massai, *Fischer* in 1882–1883 (B) m.v. 1; Kilimanjaro, Fan, Mashami, 1500 m, *Haarer 1031c* (Amani).

Minor Variants of *C. scaposa eximia*

1. Plants resembling subsp. *typica* in size, scapes only 0.4–0.5 dm high; caudical leaves and pubescence on involucre intermediate between subsp. *typica* and *eximia*. The inner involucral bracts, however, approach those of subsp. *eximia* in depth of color; and the anther tubes are abortive, being less than 2 mm long and apparently quite devoid of pollen. It is thought that the irregularities in structure of the anther tube in typical plants indicate a tendency to abortion and that the condition found in this variant is an extreme expression of this tendency. Except for the rather large leaves, dark involucres, and abortive anthers, this variant could as well have been referred to subsp. *typica*, as an intergrade toward subsp. *eximia*. *Fischer* in 1882–1883 (B), Massai, Tanganyika Terr.

2. Florets and achenes shorter than in most forms of this subspecies; corolla 9 mm long, the tube pubescent with short papilliform and long acicular hairs; achenes 4.5–5 mm long. The caudical leaves are mutilated but apparently they resemble those typical of this subspecies; the anther tubes are also typical, being about 2.75 mm long, with long filaments and unequal acuminate appendages; style branches 0.8–0.9 mm long. *Dümmer 1681* (K), grassland, 2121 m, Limora (= Limuru Station f), Kenya.

46, *c. Crepis scaposa afromontana* (R. E. Fr.) comb. nov. Plant usually taller than in subsp. *typica*, being more like subsp. *eximia*, but the rosettes usually small,



Fig. 80. *Crepis scaposa eximia*, from type (Upsala): a-c, plants, $\times \frac{1}{2}$; d, head, $\times 2$; e, floret lacking ovary, $\times 4$; e', detail of ligule teeth, $\times 50$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h-j, 2 achenes and a pappus seta, $\times 8$.

like those in the former; caudical leaves 2–9 cm long, 0.5–1.4 cm wide, very shortly petioled or sometimes elongated-petiolate; stems 0.4–3 dm high, 1–2-headed; involucre 9–11 mm long, 5–6 mm wide at middle; outer bracts 7–8, unequal, $\frac{1}{2}$ – $\frac{2}{3}$ or $\frac{3}{4}$ as long as inner bracts, 0.75–1.5 mm wide, lance-linear, obtuse, dark brown or green, glabrous or, like the 14–18 inner bracts, pubescent with short or long black glandular or glandless hairs, \pm pubescent on inner face; corolla 11.5–15 mm long; ligule 1–1.75 mm wide; teeth 0.1–0.6 mm long, gland-crested, labiate-capitate; corolla tube 3–5 mm long, beset with minute papilliform hairs and sometimes a few short acicular hairs near summit; anther tube (3) 3.75×0.9 mm dis.; appendages 0.6–0.75 mm long, oblong, obtuse; filaments 0.5–1 mm longer; style branches 1–1.75 mm long, 0.1 mm wide; achenes 4–6 mm long, 0.5–0.8 mm wide; pappus 5–6 mm long. Flowering Jan.–Feb. and June–Sept. See fig. 81.

Crepis scaposa var. *afromontana* R. E. Fr., *op. cit.*, 361.

Local on Mt. Kilimanjaro, in Kenya Colony, and in Uganda.

Tanganyika: Mt. Kilimanjaro, Marangu dist., middle altitude of the Mawenzi, mountain meadows, upper half of the virgin forest, 2440 m, *Volkens 793* (B) type; Kilimanjaro, camp, 4500 m, *Grote 3956* (B, Amani); Kilimanjaro, Peter's hut, 3726 m, occurring to 4090 m, *Greenway 3733* (UC). **Kenya:** Athi plains, 1500 m, dry places, *Mettam 240* (K), exceptional, considering the low elevation of this station; Mt. Aberdare, Sattima, high steppe and alpine reg., 3000–3500 m, *Fries 2487a, 2451a* (Upsala) m.v. 3. **Uganda-Kenya:** Mt. Elgon, grassland, 3636 m, *Battiscombe 674* (K); Mt. Elgon, Bulambuli, short grassland, 3030 m, *Snowden 919* (K); Mt. Elgon, crater, swards, 3939 m, *Dümmer 3368* (K, B); Mt. Elgon, mountain slope, 3333 m, *Lindblom* in 1920 (Stockholm); *ibid.*, *Mrs. Tweedie 26* (K). **Uganda:** above Butandiga, 2727 m, *Liebenberg 1607* (K).

Minor Variant of C. scaposa afromontana

3. Resembles subsp. *typica* in size of plants and florets and in that the flower parts are small; rosettes 0.6–0.9 dm wide; stems 0.6–0.8 dm high; corolla 8 mm long; ligule 0.8 mm wide; corolla tube 3.5 mm long, strongly pubescent at summit of tube and base of ligule with acicular hairs up to 1 mm long; anther tube 2 mm long; appendages 0.4 mm long, acute; style branches 0.9 mm long. The leaves, however, are more strongly dentate than in all specimens of subsp. *typica* at present available, and the involucre is dark and pubescent with fine black hairs more like those in subsp. *afromontana*. The small size of these plants may be due to the environment, but the smallness of the florets and flower parts can hardly be explained on that basis. This is a connecting form between subsp. *typica* and *afromontana*. *Fries 2451a, 2487a* (Upsala), alpine meadows, 3000–3500 m, Sattima, Mt. Aberdare, Kenya.

46, *d. Crepis scaposa taraxaciformis* (R. E. Fr.) Bab., Univ. Calif. Publ. Bot. 19: 403. 1941. Plant usually more robust than subsp. *typica*, but reduced specimens sometimes quite as small; caudical leaves numerous, up to 13 cm long, 2 mm wide, with a short or elongated petiole, dentate to runcinate-pinnatifid in robust specimens; stems 0.3–3 dm high, 1-headed; involucre 9–13 mm long, 7–10 mm wide at middle, of 3–5 unequal series of imbricate bracts and several subtending ones, completely glabrous or tomentulose at base, subtending bracts elongated, linear, yellow; involucre bracts 20–40, oblong, outermost acute, innermost acuminate, all obtuse and ciliate at the apex, with a dark median dorsal nerve on a greenish-yellow mid-region, much darker at margins and apex, ventrally strongly appressed-pubescent; receptacle areolate, fimbriate, glabrous; corolla 9–11 mm long; ligule 1–1.25 mm wide; teeth 0.15–0.5 mm long, narrow, prominently gland-crested and with a thin anterior comb-shaped projection; corolla tube 3.5–5 mm long, pubescent with short papilliform hairs and, sometimes near base of ligule, with a few coarse several-celled acicular hairs up to 1 mm long; anther tube 2.25×0.75 mm dis.; appendages unequal, 0.3–0.5 mm long, lanceolate, acute; filaments 0.5–0.75 mm longer; style branches 0.5–0.9 mm long, 0.07–0.1 mm wide; achenes 6–7 mm long, 0.5–0.8 mm

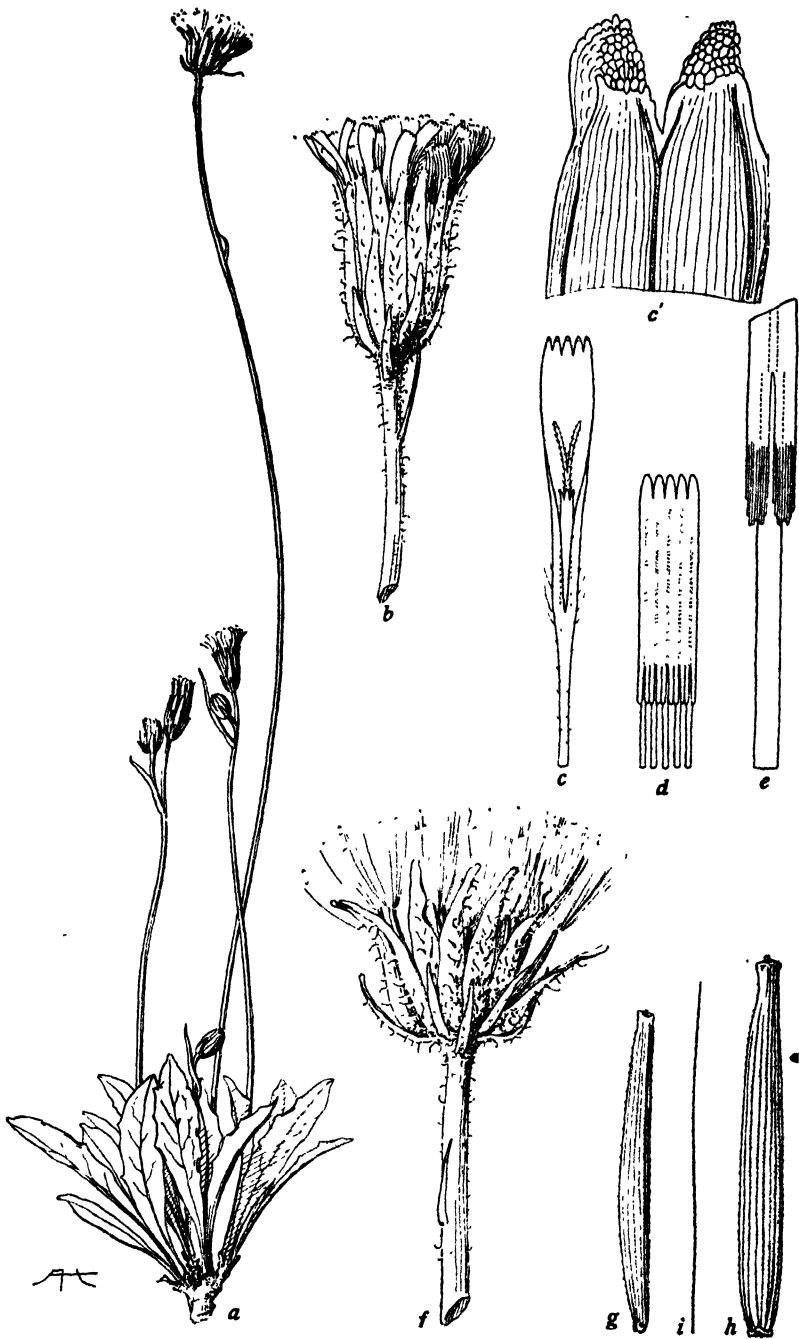


Fig. 81. *Crepis scaposa afromontana*, from Lindblom in 1920 (Stockholm): *a*, plant, $\times \frac{1}{2}$; *b*, flowering head, $\times 2$; *c*, floret lacking ovary, $\times 4$; *c'*, detail of ligule teeth, $\times 50$; *d*, anther tube, $\times 8$; *e*, detail of appendages, $\times 32$; *f*, fruiting head, $\times 2$; *g-i*, 2 achenes and a pappus seta, $\times 8$.

wide; pappus 5 mm long. Flowering Jan.–Mar., and Nov. Chromosomes, $2n = 8$. See fig. 82.

Crepis scaposa var. *taraxaciformis* B. E. Fr., *op. cit.*, 362, Pl. VII, f. 2.

This is the most variable and the most widely distributed of the 4 subspecies. It is found locally in S. Kenya Colony and the Kivu dist. in E. Belgian Congo. Presumably it occurs in Uganda. It is said by Fries (*loc. cit.*) to be a "Characterart" on the plateau of Mt. Aberdare in the upper bamboo reg.

Kenya: Mt. Aberdare (southwest of Mt. Kenya), near Sattima, grassy steppe, 3000–3500 m, *Fries 2487* (Upsala) type; *ibid.*, upper bamboo reg., open place, 3000 m, *Fries 2264* (Upsala); *ibid.*, alpine reg., *Fries 2592* (Upsala); Mt. Kenya, E. side, between Kaseri and Churi, grassy place, *Fries 1837a* (Upsala) m.v. 4. **Kenya or Tanganyika** (?): Virunga Mts., Niragongo Volcano, floor of great extinct southern crater, in sedge and moss, about 2700 m, *Burt 3189* (K, Amani) m.v. 5. **Belgian Congo** (eastern): N. Kivu (= Ruanda Prov.), clearing in mixed forest of bamboo, southeast of Karisimbi, west of Lake Kalago, 2300 m, in short grass, among lava rocks, *Mildbraed 1641* (B) m.v. 6; Ruanda Prov., S. Karisimbi, Kihorve, 2400 m, *de Witte 2284, 2290* (Brussel) near m.v. 6.

Minor Variants of C. scaposa taraxaciformis

4. Involucres with fewer bracts than in typical subsp. *taraxaciformis*, and the bracts somewhat paler, not showing obviously the color pattern so characteristic of this subspecies. The bracts, however, are dark, and on close examination are found, at least in some heads, to have the same pattern as in other plants of this subspecies, although it is not very distinct. Also, there are 16–25 bracts in 3–4 series, and the florets and all flower parts are typical. But the achenes are slightly shorter and less strongly attenuate than in the type of subsp. *taraxaciformis*. (Cf. Fries, *op. cit.*, Pl. VI, f. 3.) *Fries 1837a* (Upsala), grassy place between Kaseri and Churi, E. side of Mt. Kenya.

5. Plants rather small and slender, superficially resembling plants of subsp. *afromontana*; rosettes 0.6–1 dm wide, caudical leaves obscurely denticulate, with short narrow petioles; stems 0.3–1.1 dm high, very slender; involucres 8–10 mm long, 4–6 mm wide at middle, with only 16–25 bracts in 3–4 series. In some of the heads, however, the bracts show strikingly the characteristic color pattern of subsp. *taraxaciformis*, and the florets, flower parts, and achenes are quite characteristic of this subspecies. *Burt 3189* (K, Amani), in sedge and moss on floor of great extinct S. crater of Niragongo Volcano, Virunga Mts., Kenya (?) or Tanganyika (?).

6. Leaves mostly with longer narrower petioles; involucres with somewhat fewer bracts, mostly in 3–4 series; one plant, atypical of this subspecies, has a few short black hairs on some involucre bracts, and the stem has a linear leaf 7 cm long only 3.5 cm below the head; another plant, also atypical, has some yellow glandless hairs on the leaves; achenes are lacking. The florets and flower parts, however, are quite typical of subsp. *taraxaciformis*. *Mildbraed 1641* (B), bamboo forest, southeast of Karisimbi, west of Lake Kalago, N. Kivu, E. Belgian Congo.

Relationship

Crepis scaposa resembles *C. carbonaria* and *C. Ellenbeckii* in size and general habit, but plants of *C. scaposa* are easily distinguished by the scapiform flower stems, which are 1-headed or never more than 2-headed. From *C. carbonaria* it is sharply set off by the much larger florets and flower parts. This holds true for most forms of *C. Ellenbeckii*, in which the anther appendages in particular are only about 0.25 mm long, whereas in *C. scaposa* they range from 0.3 to 0.75 mm and are usually 0.4 mm or more. Also, in *C. Ellenbeckii* the heads are smaller, with narrower involucres, and the involucre bracts are glabrous on the inner face, whereas in *C. scaposa* they are usually pubescent within. Tall robust specimens of *C. scaposa taraxaciformis* show some resemblance to *C. glandulosissima*, but the latter has 2-headed stems which have not been found in subsp. *taraxaciformis*; and *C. glandulosissima* differs in all details of the involucre, florets, and fruits, as well as in its glandulosity.



Fig. 82. *Crepis scaposa taraxaciformis*, a-m, from type (Upsala); n-r, from Fries 2264 (Upsala); s, from hort. genet. Calif. 3301 (grown from seeds received from Dr. E. Soderberg, Stockholm, original collection by R. E. Fries on Mt. Aberdare): a, plant, $\times \frac{1}{2}$; b-d, leaves, $\times 1$; e, flowering head, $\times 2$; f, floret lacking ovary, $\times 4$; f', detail of ligule teeth, $\times 50$; g, anther tube, $\times 8$; h, detail of appendages, $\times 32$; k-m, achene, lateral and ventral views, and a pappus seta, $\times 8$; n-r, inner involucral bracts, inner face, $\times 4$; s, somatic chromosomes, $n = 4$, $\times 1250$.

47. *Crepis glandulosissima* R. E. Fr.

Svensk Bot. Tidskr. 22: 359, 1928. (Fig. 83.)

Perennial, about 5 dm high; root straight ?, elongated ?, woody, 6–7 mm wide; caudex 10–15 mm wide, covered with dark brown bases of old leaves; caudical leaves up to 16 cm long, 2 cm wide, narrowly oblanceolate, rounded-obtuse, minutely apiculate, remotely sinuately denticulate, dentate or lobed, attenuate into a winged petiole with broader base, setuliferous on both sides with pale yellow setules 0.5 mm long bearing minute dark brown or purple glands, like stem purplish toward base; one cauline leaf about midway at bifurcation, 3.5–4 cm long, 0.5 cm wide, linear, acuminate, sessile, gland-setulose; stems 1 or 2, erect, scapelike, simple or 1–2-furcate, 1–3-headed, terete, fistulose, striate, shortly and finely gland-pubescent, sparsely below, densely above; peduncles 0.5–20 cm long, stout, 1–3-bracteate, bracts overlapping and simulating outer bracts of involucre, slightly thickened near base of head in fruit, fuscous-tomentose, densely gland-pubescent; heads erect, medium, many-flowered; involucre campanulate, 12 mm high, 8 mm wide in anthesis, broadly cup-shaped in fruit; outer bracts 7–8, unequal, $\frac{1}{2}$ – $\frac{3}{4}$ as long as inner bracts, linear, acute or acuminate, tomentose, densely gland-hairy along margin near tip, hairs brown or black; inner bracts 12–14, lanceolate, obtuse, white-ciliate at apex, in 2 ranks, inner ones broadly membranous-margined, ventrally strigulose with yellowish shining hairs, dorsally tomentose, gland-hairy with yellow, brown, or black unequal hairs, the bracts becoming strongly carinate, spongy-thickened in fruit; receptacle areolate, glabrous; corolla 9 mm long; ligule 1 mm wide; ligule teeth 0.1–0.15 mm long; corolla tube 3 mm long, beset with minute papilliform 3–4-celled trichomes, and at base of ligule, with tortuous 3–4-celled acicular hairs up to 0.05 mm long; anther tube 2.8×0.9 mm dis.; appendages 0.7 mm long, oblong, acute; filaments unequal, 0.4–0.8 mm longer; style branches 1 mm long, 0.1 mm wide, yellow; achenes (immature) 4.5–5 mm long, pale brown, fusiform, narrowed above the hollow strongly calloused base, strongly attenuate to the narrow summit, with slightly expanded pappus disk, 20-ribbed, ribs close, narrow, rounded, very faintly and finely muriculate; pappus white, 5 mm long, 2-seriate, rather fine, soft, deciduous. Flowering Feb.; flowers yellow.

British E. Africa, Kenya Prov., on short grassland at an elevation of 2100 m or higher.

Monomorphic.

Kenya Colony: Kenya Prov., N. side of Mt. Kenya, grass-covered hills between Marania and Jarauma R., *Fries 1546* (Upsala) type; Kenya Prov., near Limuru railway station, 2121 m, *Snowden 561* (K).

Relationship

This species is closest to *C. scaposa*, from which it is easily distinguished by the glandular indumentum of the leaves and stem, the usually somewhat larger heads, the dense glandular pubescence of the involucre, and the inner involucre bracts strigulose on inner face.

48. *Crepis ugandensis* sp. nov.

(Fig. 84.)

Herba perennis (?) 5–9 dm alta; caudex rectus ligneus ad summitatem foliatus; folia caudicalia erecta elongata anguste oblanceolata dentata petiolata puberula vel glabra; folia caulina similia plerumque reducta linearia vel bracteiformia; caules tenues fistulosi glabrati 2–3-ramosi, ramis remotis strictis elongatis cymosis; capitula pauca parva circa 35-flora; involucrea cylindrico-campanulata 7–8 mm longa ad basim 3–4 mm lata, tomentosa glandulosa-pubescentia et breve nigro-setosa, squamis



Fig. 83. *Crepis glandulosissima*, from type (Upsala): a, plant, $\times \frac{1}{2}$; b, stem and peduncles, $\times \frac{1}{2}$; c, caudical leaf, $\times 1$; d, heads in anthesis, $\times 2$; e, floret lacking ovary, $\times 4$; e', detail of ligule teeth, $\times 50$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, i, immature achene and a pappus seta, $\times 8$; k, k', inner involucral bract, outer and inner face, $\times 4$.

exterioribus 5 inaequalibus linearibus, interioribus 8–10 oblongis acutis necnon in fructu incrassatis; receptaculum alveolatum; corolla 10–11 mm longa, ligula 7 mm longa 1.5 mm lata flava in dorso rubescenti; antherae 4 mm longae; rami styli 2.75 mm longi flavi; achaenia fusca 5.5–6 mm longa circa 0.5 mm lata breve rostrata 13-costata; pappus pallido-flavidus 5–6 mm longus 3-seriatus persistens.

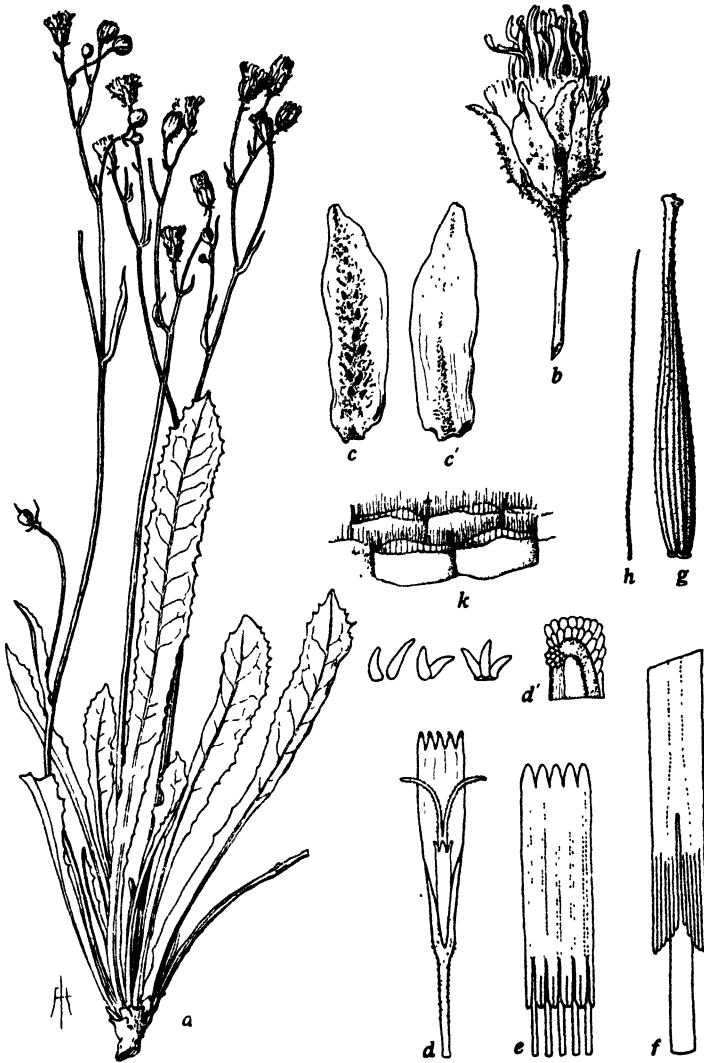


Fig. 84. *Crepis ugandensis*, from type (K): a, plant, $\times \frac{1}{4}$; b, flowering head, $\times 2$; c, c', inner involucral bract, outer and inner faces, $\times 4$; d, floret lacking ovary, $\times 4$; d', hairs from corolla tube, $\times 50$, and detail of ligule tooth, $\times 25$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, h, achene and a pappus seta, $\times 8$; k, detail of receptacle, $\times 25$.

Perennial (?), 5–9 dm high; caudex 0.8–1.5 cm wide, abruptly constricted into a slender taproot; caudical leaves up to 27 cm long, 2.7 cm wide, erect or ascending, narrowly oblanceolate, acute or somewhat obtuse, apiculate, closely and irregularly dentate, teeth triangular and mucronate, gradually attenuate into a long winged petiole, puberulous with minute appressed glandless hairs, especially on lower face; lower cauline leaves similar but reduced, middle and upper ones linear-acumi-

nate or bractlike; stems 2–3, erect, slender, terete, fistulose, striate, glabrous, 2–3-branched, branches remote, strictly erect, the lowest from near base, elongated, few-headed, aggregate inflorescence a compound cyme; peduncles 2–9 cm long, sparsely setulose, longer ones 1–2-bracteate; heads erect, small, about 35-flowered; involucre cylindric-campanulate, 7–8 mm long, 3–4 mm wide at base in fruit, fuscous-tomentose, gland-pubescent with short white hairs bearing brown glands, and setose with short black blunt setae on inner bracts; outer bracts 5, unequal, longest $\frac{1}{2}$ as long as inner ones and nearly 1 mm wide at base, lance-linear, acuminate; inner bracts 8–10, oblong, acute or acuminate, rounded and white-ciliate at apex, with narrow dark median dorsal stripe and broad pale brown scarious borders, under lens \pm pubescent on inner face with very short shining hairs, becoming indurate but not much thickened at base; receptacle alveolate, fimbriellae 0.25 mm high, shortly and finely ciliate; corolla 10–11 mm long; ligule 1.5 mm wide; teeth 0.5 mm long; corolla tube 3–4 mm long, beset with very short (up to 0.12 mm long) papilliform hairs arranged singly or in clumps; anther tube 4×1.1 mm dis.; appendages 0.8 mm long, oblong, sagittate; filaments 0.75 mm longer; style branches 2.75 mm long, 0.15 mm wide, yellow; achenes brown, 5.5–6 mm long, 0.5 mm wide, gradually attenuate into a beak about 1 mm long and 0.15–0.2 mm wide, with abruptly expanded pappus disk 0.3–0.4 mm wide, constricted at the white-calloused hollow base, 13-ribbed, ribs nearly equal or 3 somewhat stronger, narrow, rounded, spiculate, especially toward the apex, spicules white; pappus yellowish-white, 5–6 mm long, 3-seriate, rather fine, soft, persistent. Flowers yellow, with reddish-purple dorsal stripe on ligules.

Known only from the type locality in W. Uganda.

Monomorphic.

Uganda: Ft. Portal, Toro, short grassland, 1666 m, *Snowden 86* (K, UC 482461) type, isotype.

Relationship

Crepis ugandensis is closest to *C. Swynnertonii*, but, with the exception of the achenes, which are similar, is distinct from it in nearly every vegetative and floral feature.

49. *Crepis Swynnertonii* S. Moore

Jour. Bot. 54: 285. 1916. (Figs. 85, 86.)

Perennial, 6–7+ dm high; caudex 1 cm wide, swollen to 2 cm wide at the leafy crown; caudical leaves up to 18 cm long, 4.5 cm wide, oblanceolate, obtuse, cuspidate, sinuate-dentate, gradually attenuate into a winged petiole with clasping base, glabrous; lowest cauline leaves (near base) similar or sessile, the others small, linear or bractlike; stems erect, robust, up to 5 mm wide at base, sulcate or striate, glabrous, paniculately branched from near base, branches remote, elongated, few-headed, aggregate inflorescence cymose-corymbiform; peduncles 1.5–6.5 cm long, slender, glabrous or tomentulose near head, 1–3-bracteate; heads erect, rather small, about 20-flowered; involucre cylindric-campanulate, 7–9 mm long, 3–4 mm wide at base in fruit, canescent-tomentulose; outer bracts 9, with 2–3 subtending ones, unequal, longest $\frac{1}{2}$ as long as inner ones, linear-subulate, 0.3–0.4 mm wide at base, becoming carinate, scarious and lax; inner bracts 13, lanceolate, obtuse, white-ciliate at apex, innermost broadly membranous-margined, glabrous on inner face, mediodorsally brown nerved, becoming somewhat carinate and indurate, not spongy-thickened; receptacle fimbriate, fimbriellae dark brown; corolla 11.5 mm long; ligule 1.2 mm wide; teeth 0.2–0.3 mm long, obtuse; corolla tube 4.75 mm long, pubescent with acicular 2-celled hairs up to 0.2 mm long; anther tube about 3×1



Fig. 85. *Crepis Swynnertonii*, from type (BM) : a, a', lower and upper parts of the plant, $\times \frac{1}{2}$.

mm dis.; appendages 0.4 mm long, acute; filaments slender, 1.25 mm longer; style branches 1.2 mm long, 0.1 mm wide, yellow; achenes purplish-brown, 5–6 mm long, about 0.7 mm wide, fusiform, \pm compressed, strongly attenuate near the apex, 0.3 mm wide just below the scarcely expanded pappus disk, abruptly constricted at the pale-calloused hollow base, 15–16-ribbed, ribs rather close, narrow, nearly equal, strongly spiculate toward the apex; pappus yellowish-white, 6 mm long, 2-seriate, nearly equal, rather fine, soft, persistent. Flowering June–July; flowers yellow.

Northern Rhodesia, in Nyasaland Protectorate and adjacent districts, mountains, and plateaus; and in N.E. Belgian Congo, savannas. Unfortunately the type locality, as published, "Rhodesia, near Chipete," is indefinite. Although Moore (*loc. cit.*)

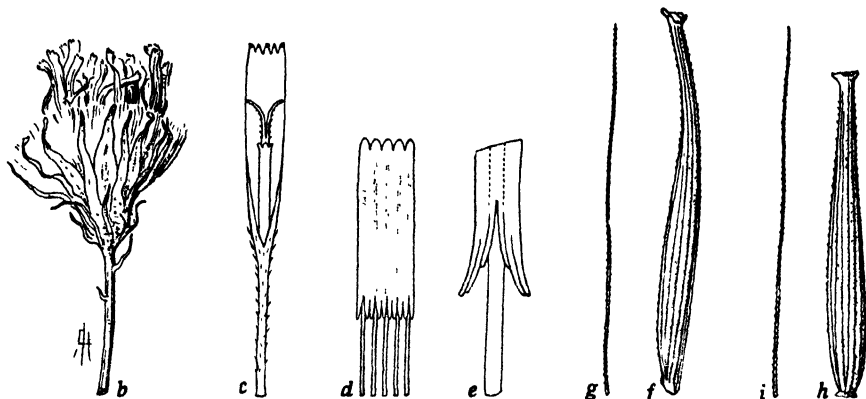


Fig. 86. *Crepis Swynnertonii*, b–g, from type (BM); h, i, from *Whyte*, "Hondowe to Haronga" (K): b, flowering head, $\times 2$; c, floret lacking ovary, $\times 4$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f–i, 2 achenes and pappus setae, $\times 8$.

gives Rhodesia, Swynnerton's label reads Gazaland, which is in S. Portuguese E. Africa. But neither Stielers nor the Times Atlas gives "Chipete" (Moore's spelling) or any similar place in Gazaland. The Times Atlas does show a "Chipeta" in Portuguese E. Africa just south of the border between Nyasaland and Tete; and Stielers Atlas gives "Chipata" in the Muchinga Mts. of Northern Rhodesia west of Nyasaland. Since 3 localities in Nyasaland are known, 2 in the north and the other in the south, the type locality may be either Chipeta or Chipata; but the latter seems the more likely guess, since Swynnerton's script suggests "Chipate," and since a variant of this species is now known from N.E. Belgian Congo, an important northern extension of the range.

Nyasaland Protectorate: N. Nyasa, S. Nyika Mts., 1212–2121 m, *Whyte* in 1896 (K); N. Nyasa (?), Hondowe to Haronga (= Kondowe = Livingstonia ? to Karonga ?), *Whyte* (K); S. Nyasaland, Zomba (west of Lake Chilwa), Shiki (= Shire ?) Highland, top of Zomba, *Buchanan 1411* (K). "Gazaland, near Chipete": Grazed pasture, *Swynnerton* in 1912 (BM, Ucf) type. **Belgian Congo:** Orientale, Ituri dist., west of Lake Albert–Nyanza, between Irumi and Bogoro, grassy savanna, *Bequaert 4912* (Brussel) m.v. 1; Tshitirunge, ancient cave, *Bequaert 5994* (Brussel) m.v. 1.

Minor Variant of C. Swynnertonii

1. Less robust, the single stem branched only toward the summit; the involucre scabridulous; and the achenes a little longer, with fewer ribs. This form differs from the type in the following details: caudex 0.5 cm wide; caudical leaves up to 6 cm wide; stem about 2 mm wide at base; peduncles up to 9 cm long; involucre setulose, with short black glandless setules; corolla about 10 mm long; ligule 1.5 mm wide; corolla tube 3.5 mm long, pubescent, with papilliform and acicular hairs up to 0.1 mm long; filaments 1 mm long; achenes 7–8 mm long, 10–12 ribbed. *Bequaert 4912* (Brussel), grassy savanna between Irumi and Bogoro, Ituri dist., N.E. Belgian Congo; *Bequaert 5994* (Brussel), ancient cave, Tshitirunge, Belgian Congo.

Relationship

Crepis Swynnertonii is closest to *C. simulans* and *C. Newii bumbensis* but is very distinct from both in the following respects: large size of the plant and the leaves, absence of pubescence, except tomentum on peduncles and involucre and setules on the involucre in m.v. 1, much smaller heads with very narrow outer involucral bracts, narrower ligules, longer style branches, and less attenuate achenes. Although only one notable variant is known thus far in this species, the locality for m.v. 1 is about 1300 km north of the other most northern known localities for the species. Hence, it is not improbable that further collections in the intervening region will reveal the existence of still other variants of this species.

50. *Crepis subscaposa* Collett et Hemsl.

Jour. Linn. Soc. 28: 78. 1891. (Fig. 87.)

Perennial, 2–4(6) dm high; taproot long, vertical, woody or somewhat fleshy; caudex about 5 mm long, 5 mm wide, leafy, bearing 1–3 flower stems; caudical leaves few, rosulate, largest 5–9 cm long, 1.8–3 cm wide, oblanceolate to elliptic, obtuse or acute, finely and irregularly denticulate, gradually attenuate into a short winged petiole, broader at base, densely pubescent on both sides with short fine gland hairs; cauline leaves few, remote, small, linear, acuminate, or bractlike; stem erect, terete, striate, not fistulose, sparsely tomentulose, \pm gland-pubescent or glabrescent, cymosely 1–3-branched toward summit, branches 1–2-headed; peduncles 0.3–4 cm long, slender, bracteate, densely gland-pubescent, scabridulous or sparsely tomentulose; heads erect, medium, many-flowered; involucre in fruiting heads campanulate, 7–10 mm long, 4–6 mm wide at middle, sparsely tomentulose, sometimes densely gland-pubescent, sometimes with very short black setules on inner bracts; outer bracts 5–8, unequal, longest about $\frac{1}{2}$ as long as inner ones, linear, acute, becoming lax; inner bracts 12–15, lanceolate, obtuse, glabrous within, becoming dorsally carinate, indurate, and somewhat spongy-thickened at base; receptacle areolate-fimbriate, fimbriae 0.2–0.5 mm high, sometimes lacinate; corolla 11–12 mm long; ligule 1 mm wide; teeth 0.25–0.4 mm long; corolla tube 4.5–5 mm long, relatively wide, like lower part of ligule beset with stout papilliform hairs 0.1 mm long; anther tube 3×0.9 mm dis.; appendages 0.6 mm long, acute; filaments short; style branches 1.75 mm long, slender, yellow; achenes dark brown or purplish, 5–6.5 mm long, 0.7 mm wide, subterete, narrowly fusiform, strongly attenuate to summit, with slightly expanded pappus disk, constricted above the white-calloused hollow base, 10–12-ribbed, ribs nearly equal, rounded, finely spiculate; pappus dusky white or pale yellow en masse, 5–6.5 mm long, 2-seriate, fine to medium, soft, persistent. Flowering Apr.–May; flowers yellow.

N.W. Burma, S.W. Yunnan, and W. Indo-China (Laos), in mountains from 900 to 2200 m. Probably in N. Siam.

Monomorphic.

Burma: Shan Hills, Tamakan, 909 m, Collett in 1888 (K, UCf) n. 574 = type; Kalau, Dickason 1031 (G). **Yunnan:** Szemao, "S.W. Mts.," 1818 m, Henry 13004 (K, NY, Mo); moist pastures on hills west of Tengueh, 25° N., 1818 m, Forrest 7608 (K); Lan Tsang Hsien, field, 1400 m, Wang 76531 (G); Shung-Kiang Hsien, mountain slope, 2200 m, Wang 73108 (G). **Indo-China:** Laos, Xieng Khouang Prov. (Tran Ninh), "plaine des Jarres," 1100 m, Petelot in 1931 (NY).

Relationship

Although referred by Collett and Hemsley (*loc. cit.*) to sec. *Youngia* under *Crepis*, *C. subscaposa* is not related to any of the species accepted in *Youngia* by

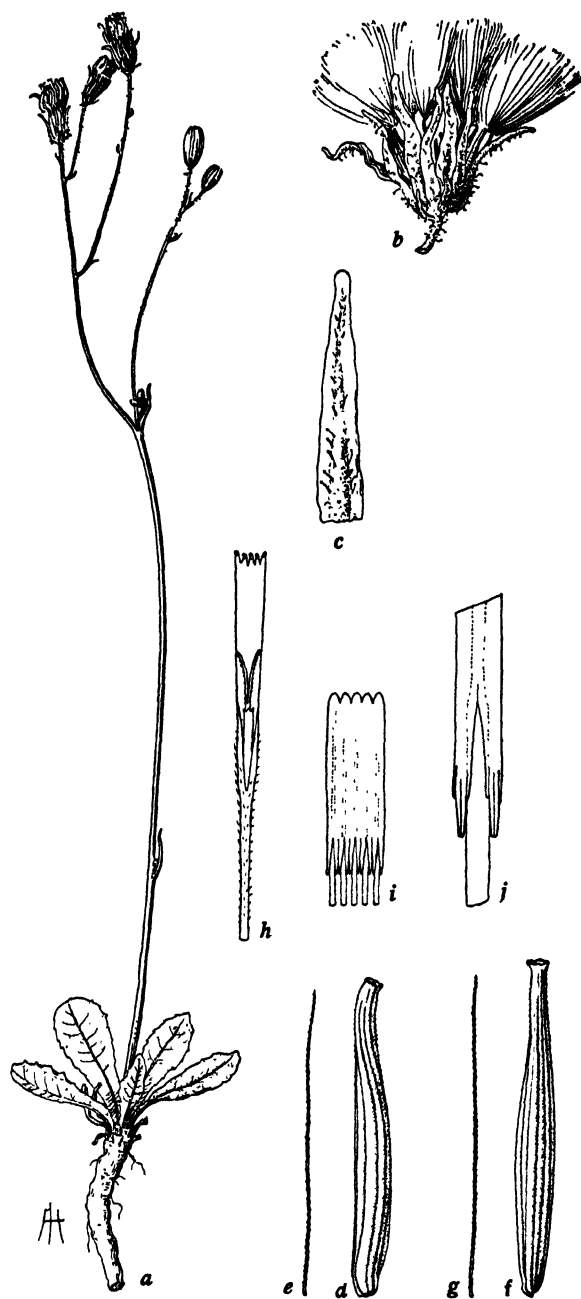


Fig. 87. *Crepis subscaposa*, a, f-i, from Henry 13004 (K); b-e, from type (K): a, plant, $\times \frac{1}{2}$; b, mature head, $\times 2$; c, inner involucre bract, outer face, $\times 4$; d-g, achenes and pappus setae, $\times 8$; h, floret lacking ovary, $\times 4$; i, anther tube, $\times 8$; j, detail of appendages, $\times 32$.

Babcock and Stebbins (B. and S., 484). Neither can it be considered as *Hieracium* on any account. Apparently this little-known species is most closely related to certain species of sec. 8, especially *C. Newii*, which also has the inner bracts of fully mature involucre somewhat spongy-thickened at the base. It seems very probable, therefore, that *C. subscaposa* represents a line derived from the same primitive stock from which the *Crepis* species of tropical Africa were derived. This view is consistent with the hypothesis that the center of origin for *Crepis* was in Central Asia.

Although *C. subscaposa* resembles *C. napifera* (sec. 17), which is also of S.E. Asia, in the strong perennial root, in the few broad obtuse caudical leaves, and in the single erect nearly leafless stem, yet in type of inflorescence, in size of heads and number of florets, in involucral characters and surface of the receptacle, as well as in the flowers and fruits, the two species are very different. Apparently they represent two lines which arose from the same stock and have diverged rather widely in morphology.

51. *Crepis simulans* S. Moore

Jour. Bot. 54: 286. 1916. (Fig. 88.)

Perennial, up to 3 dm tall; taproot straight, thick, woody; caudex simple or divided; caudical leaves ascending, up to 8 cm long and 1.8 cm wide, oblanceolate, obtuse, attenuate into a very short winged petiole, acutely dentate, glandular-hispidulous on both sides; lower cauline leaves narrower, sessile, amplexicaul, acute; upper cauline leaves linear or bractlike; stems 1–4 to a caudex, erect, terete, fistulose (?), sulcate or striate, densely hispid, cymosely few-branched from near base upward, branches 1–2-headed, aggregate inflorescence corymbiform; peduncles stout, erect or arcuate, hispidulous; heads erect, medium, many-flowered; involucre in anthesis cylindrical, about 10 mm high, 4–5 mm wide, in fruit campanulate, about 13 mm high, 7 mm wide, ultimately reflexed; outer bracts 8, lance-linear, acuminate, longest $\frac{1}{2}$ as long as the inner, like inner bracts canescent-tomentose, gland-pubescent, and hairy; inner bracts 12–14, lanceolate, obtuse, white-ciliate at tip, densely hairy near apex with dark glandless setiform hairs, glabrous within, becoming rounded-carinate near base, not indurate nor spongy-thickened; receptacle areolate-fimbriate; corolla 10.5 mm long; ligule 1 mm wide; ligule teeth 0.2–0.4 mm long; corolla tube 3.5 mm long, beset with papilliform hairs 0.05–0.1 mm long; anther tube about 3×0.9 mm dis.; appendages 0.4–0.5 mm long, narrow, acute; filaments 0.75 mm longer; style branches 0.5 mm long, 0.1 mm wide, well extruded in anthesis, yellow; achenes dark brown, 6.5–8 mm long, about 0.6 mm wide, subterete, gradually attenuate into a coarse beak 2–3 mm long, with expanded yellow pappus disk and narrow yellow basal callosity, 10-ribbed, ribs well spaced, narrow, rounded, very finely spiculate; pappus 4–5 mm long, yellowish-white, 2-seriate, rather stiff, fine, persistent. Flowers yellow.

Known only from the type collection.

Monomorphic.

Southern Rhodesia: Melsetter dist. (Gazaland), Mt. Chirinda, *Swynnerton* in 1913 (BM, UCf).

Relationship

This species is closest to *C. Newii*, from which it differs in the inner involucral bracts being not spongy-thickened at maturity, in the very short style branches, and in the glandular hispidulous caudical leaves, as well as in other details. It is also close to *C. Swynnertonii*, from which it differs in the smaller gland-pubescent rosette leaves, the fewer-headed hispid stems, the larger heads, the pubescence of involucre, the shorter style branches, and the longer more definitely beaked achenes.



Fig. 88. *Crepis simulans*, from type (BM): a, plant, $\times 1$; b, flowering head, $\times 2$; c, fruiting head, $\times 2$; d, inner involucre bract, outer face, $\times 4$; e, floret lacking ovary, $\times 4$; e', detail of ligule teeth, $\times 50$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, k, l, 2 achenes and a pappus seta, $\times 8$.

52. *Crepis Gossweileri* S. Moore

Jour. Linn. Soc. 47: 282. 1925. (Fig. 89.)

Perennial, 7.5–8 dm high; caudex vertical, tapering, 1 cm wide at summit, leafy at the divided crown; caudical leaves up to 14 cm long, 2.5 cm wide, obovate, obtuse, denticulate, gradually attenuate into a long winged petiole, pubescent on both sides, especially on veins, with stiff appressed hairs; cauline leaves few, small, lance-linear or bractlike; stems 3, erect, sulcate, fistulose, cymosely 2–4-branched near summit, few-headed; peduncles 1.5–4 cm long, puberulous or tomentulose at summit;

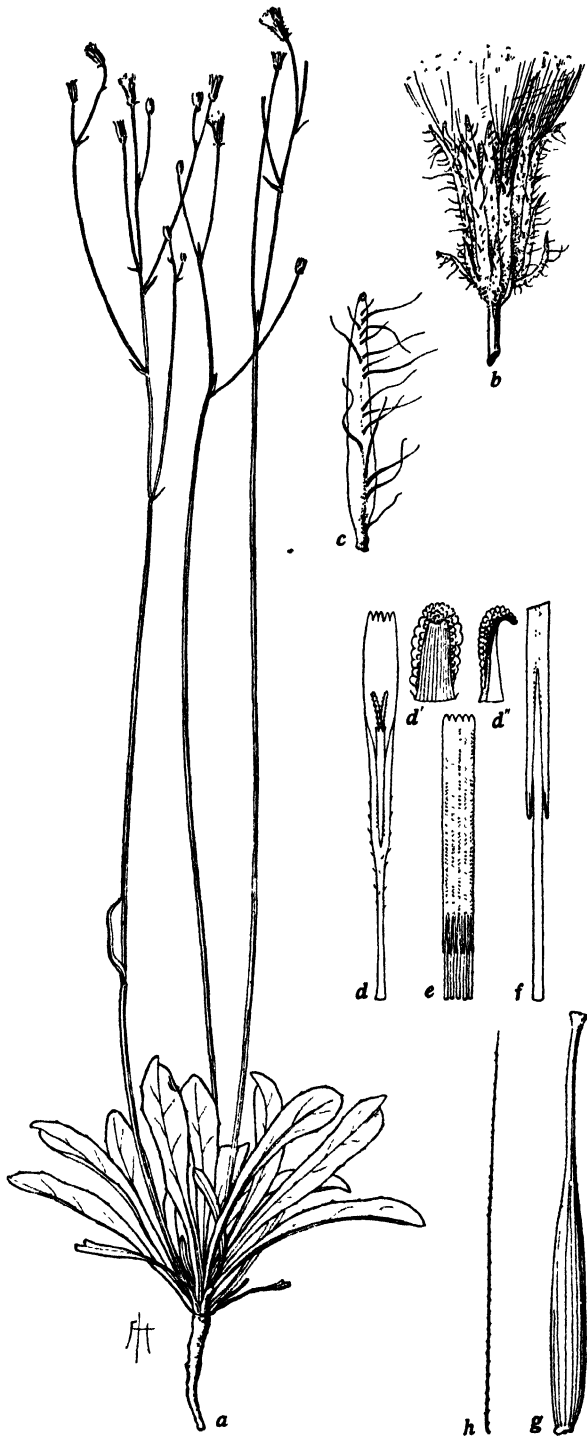


Fig. 89. *Crepis Gossweileri*, from type (BM): a, plant, $\times \frac{1}{4}$; b, immature head, $\times 2$; c, inner involucre bract, $\times 4$; d, floret lacking ovary, $\times 4$; d', d'', details of ligule teeth, inner face and lateral view, $\times 50$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, h, achene and a pappus seta, $\times 8$.

involucre 11 mm long, campanulate, canescent-tomentose, strongly setose on both outer and inner bracts with black glandless setae; outer bracts 7, narrowly linear, unequal, longest about $\frac{1}{2}$ as long as inner ones; inner bracts 13, lance-linear, obtuse or acute, glabrous on inner face, becoming indurate but not much thickened in fruit; receptacle areolate, fimbriate; corolla about 13 mm long; ligule 1 mm wide; teeth 0.2–0.3 mm long; corolla tube 5 mm long, sparsely pubescent with 1–2-celled acicular hairs 0.05–0.2 mm longer; anther tube about 4×0.5 mm dis.; appendages 0.6 mm long, narrow, lanceolate; filaments about 0.75 mm longer; style branches 1 mm long, 0.1 mm wide, yellow; achenes brown, 7 mm long, 0.7 mm wide, fusiform, strongly attenuate into a beak 0.25 mm wide and nearly equal to the body, pappus disk 0.5 mm wide, slightly narrowed to the calloused base, about 16-ribbed, ribs very narrow, finely spiculate; pappus yellowish-white, 7 mm long, 2-seriate, rather fine, soft, persistent. Flowering Feb.; flowers yellow.

Known only from the type locality, where it was collected in February, 1907, by J. Gossweiler.

Monomorphic.

Angola: near Cului, in woods composed chiefly of *Berlinia Baumii*, Gossweiler 2895 (BM).

A fragmentary specimen from S. Belgian Congo, in Herb. Hort. Bot. Bruxelles, is evidently closely related to *C. Gossweileri* but differs in the densely setulose upper stem and peduncles, the short setules on the involucreal bracts, the pubescence on inner face of the inner bracts, the smaller florets with much shorter anther tubes, and the shorter pappus. The achenes and pappus are similar, however, and until more material is available of both *C. Gossweileri* and this form, the latter's status remains in doubt.

Relationship

Crepis Gossweileri is closest to *C. Newii bumbensis*, from which it is very distinct in the tall, nearly leafless stems which are branched only near the summit, the narrower, strongly setose involucre, the narrower corollas and anther tubes, the longer beaked achenes, and the longer pappus. In its narrower involucre, unusually narrow florets, and more conspicuously beaked achenes, this species is more specialized than *C. Newii*, although the setaceous involucre merely becomes indurate and little thickened in fruit.

53. *Crepis Friesii* sp. nov.

(Fig. 90.)

Herba perennis 4.5 dm alta; caudex rectus 5 mm latus fuscus; folia caudicalia pauca 5 cm longa 1.4 cm lata elliptica vel obovata papilloso-denticulata breve petiolata superne pubescentia, pilis brevis tenuis pallidis eglandulosis; folia caulina 2 (bracteae exclusae) remota oblanceolata vel linearia; caulis rectus tenuis glabrus vel paululum scabridulus ad summitatem 2-furcatus cum 3 capitulis; pedunculi 1.2–3.5 cm longi tenuissimi cum 6–7 squamis parvis linearibus circa 0.3 mm latis capitulum subtendentibus; capitula recta parva circa 17-flora; involucrea cylindrico-campanulata 7 mm longa 3–4 mm lata nigrescentes scabra, setulis brevis eglandulosis, squamis exterioribus nullis vel summotis, squamis interioribus 9–10 lanceolatis ventrale pubescentibus in maturitate induratis sed non incrassatis; corolla 11–12 mm longa, ligula flava 6–7 mm longa 1.5 mm lata, tubo pubescenti, pilis brevissimis papilliformibus et acicularibus; antherae flavae 3.7 mm longae; rami styli 1–1.25 mm longi flavi; achaenia (paene matura) rubido-fusca 5.5 mm longa 0.75 mm lata fusiformia ad summitatem valde attenuata 0.3 mm lata 12-costata superne dense spiculata; pappus flavidus 6 mm longus 2-seriatus, setis aequalibus ad basim 33 micron latis molliusculis persistentibus.

Perennial, 4.5 dm high; caudex vertical, 5 mm wide, covered with brown bases of old leaves; caudical leaves few, up to 5 cm long, 1.4 cm wide, elliptic to obovate, mucronate, papillose-denticulate, narrowed into a short winged petiole with broader clasping base, finely pubescent on upper face with short pale glandless hairs, puberulous on lower face, especially on midrib; cauline leaves 2, excluding

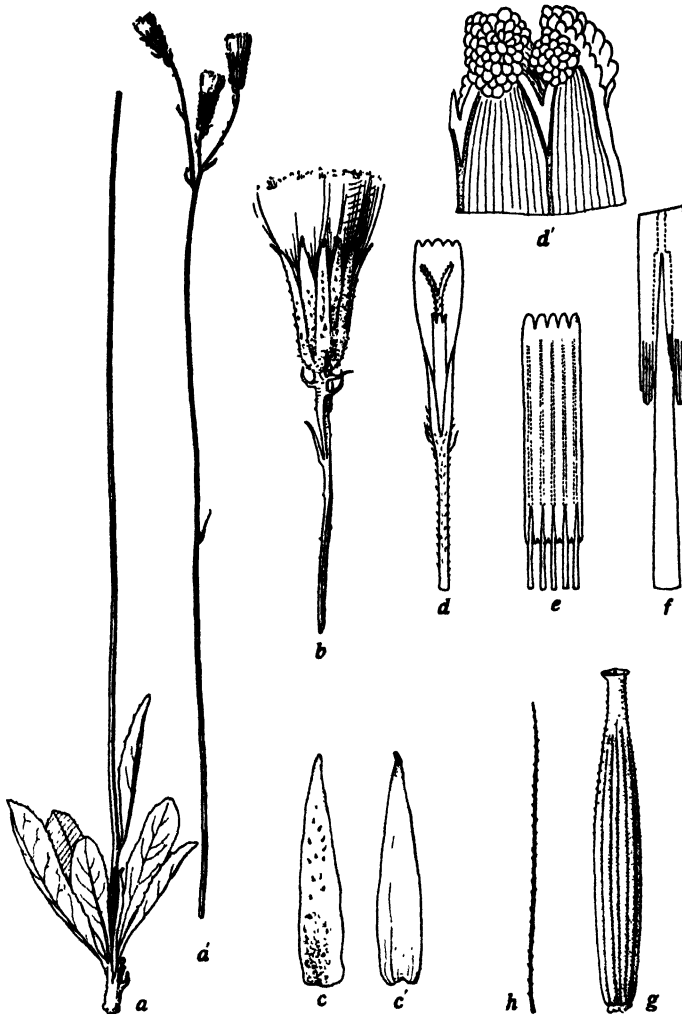


Fig. 90. *Crepis Friessii*, from type (Upsala): a, a', plant, $\times \frac{1}{2}$; b, fruiting head, $\times 2$; c, c', inner involucre bract, outer and inner faces, $\times 4$; d, floret lacking ovary, $\times 4$; d', detail of ligule teeth, $\times 50$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, h, achene and a pappus seta, $\times 8$.

bracts, the lower one 3 cm above the caudex, oblanceolate, acute, papillose-denticulate and with a pair of small narrow teeth or auricles at base of blade, very shortly petioled, the upper one 13 cm below the summit, linear, bractlike, subtending an abortive flower head; stem erect or sinuate, very slender, terete, striate, glabrous or somewhat scabridulous above, cymosely 2-furcate near summit, 3-headed; peduncles 1.2–3.5 cm long, very slender, glabrous or scabridulous, slightly thickened near head with 6 or 7 small bracts subtending the head, bracts linear, about 0.3 mm wide, scarious, lax; heads erect, small, about 17-flowered; involucre cylindric-campanulate, 7 mm long, 3–4 mm wide at middle, blackish in sic., slightly farinose

near base, scabrous with very short black glandless setules; outer bracts absent or displaced to summit of peduncle; inner bracts 9–10, lanceolate, acute or obtuse, white-ciliate at tip, membranous-margined, appressed-pubescent on inner face with short fine shining hairs, becoming indurate but not much thickened in fruiting heads; receptacle (?); corolla 11–12 mm long; ligule 1.5 mm wide; teeth nearly equal, 0.2 mm long; corolla tube about 5 mm long, densely pubescent with very short papilliform hairs and near summit a few coarse acicular hairs up to 0.5 mm long; anther tube 3.7×1 mm dis.; appendages 0.6 mm long, lanceolate, acute, united; filaments equal, 0.75 mm longer; style branches 1–1.25 mm long, 0.1 mm wide, attenuate, yellow; achenes (almost mature) reddish-brown, 5.5 mm long, 0.75 mm wide, fusiform, strongly attenuate upward to the 0.3 mm wide summit, with white pappus disk 0.4 mm wide, constricted above the prominently calloused oblique hollow base, 12-ribbed, ribs rounded, densely spiculate toward summit; pappus yellowish-white, about 6 mm long, 2-seriate, setae nearly equal in length and width, about 33μ wide at base, rather soft, persistent. Flowering Dec.; flowers yellow.

Crepis Rueppellii var. *centrali-africana* R. E. Fr., Svensk Bot. Tidskr. 22: 366. 1928.

Known only from the type specimen, which is the "specimen originale" of *C. Rueppellii* var. *centrali-africana* R. E. Fr. However, not only this, but still another species (cf. *C. Mildbraedii*) was determined by Fries as the above-named variety of *C. Rueppellii*, whereas the other two specimens cited by Fries under this variety are actually of that species.

Monomorphic.

Belgian Congo: Ruanda reg., Rusisi-Tal, mountains at south end of Lake Kivu, in short-grass meadows, about 1500 m, *Fries 1507* (Upsala, UGf).

Relationship

In the subtending outer involucre bracts, *Crepis Friesii* is very distinct from every other species of *Crepis*, but it is certainly related to several other central African species, most closely, perhaps, to *C. congoensis*. From the latter it is easily distinguished by the smaller, nearly entire leaves, the single flower stem, the much smaller heads, and the shorter unbeaked achenes, as well as by the peculiar involucre. From *C. Rueppellii* this species differs greatly in habit and leaf characters, as well as in certain floral details, especially the much shorter style branches, and most of all in the scarcely thickened involucre bracts and the reddish, unbeaked achenes. From *C. Mildbraedii* it is equally distinct in its very small, almost entire leaves, its fewer, larger heads, larger florets, and flower parts, and its larger, reddish achenes with coarser ribs and longer, equal pappus setae. Since the pollen grains are regular, 3-pored, and about 26μ in diameter, this is very probably a diploid species.

54. *Crepis Mildbraedii* sp. nov.

(Fig. 91.)

Herba perennis circa 5 dm alta; radix anguste napiformis elongata 7 mm lata; caudex 5 mm latus fuscus; folia caudalia 10 cm longa 3 cm lata elliptica obtusa irregulariter denticulata in petiolum anguste alatum attenuata pubescentia; folia caulina 2 (bracteae exclusae) 7 et 2 cm longa linearia sessilia; caulis rectus ad basim glanduloso-pubescent remote 3–5-ramosus super partem mediam, ramis strictis 1–3-capitulis; inflorescentia aggregata subcorymbiformis; pedunculi 1.5–7 cm longi tenui ad summitatem scabridulosi; capitula recta parva circa 30-flora; involucre campanulata 6–7 mm longa circa 4 mm lata tomentulosa scabridulosa, squamis exterioribus 5–6 aequalibus circa 2 mm longis et 0.4 mm latis linearibus, squamis interioribus 10 inaequalibus lanceolatis obtusis ventraliter glabris in maturitate

paululum carinatis et induratis non incrassatis; corolla 9 mm longa, ligula flava 5.5 mm longa 1 mm lata, tubo dense pubescenti, pilis breve papilliformibus et acicularibus; antherae flavae 3 mm longae; rami styli 0.75 mm longi flavae; achenia (paene matura) nigro-fusca circa 5 mm longa 0.5 mm lata \pm attenuata 10-costata, costis tenuis spiculatis; pappus flavidus 5 mm longus 2-seriatus, setis inaequalibus ad basim 15–33 micron latis, molliusculus barbellulatus persistens.

Perennial, about 5 dm high; root narrowly napiform, elongated, 7 mm wide below the contracted summit; caudex 5 mm wide, covered with brown bases of old leaves; caudical leaves up to 10 cm long, 3 cm wide, elliptic, obtuse, irregularly or retrorsely denticulate, teeth mucronate, attenuate into a narrowly winged petiole with broader clasping base, \pm pubescent on both sides with brown or yellow glandless setiform hairs and some shorter gland hairs on midvein beneath; cauline leaves 2, excluding bracts, the lower 1–3 cm above base, 7 cm long, linear, acute, denticulate, and shallowly 4-lobed near base, sessile, the upper 18–35 cm above base, subtending the first branch, 2 cm long, linear, acuminate, sessile; stem erect, terete, striate, sparsely gland-pubescent near base, glabrous above, remotely 3–5-branched above middle, branches strict, 1–3-headed, aggregate inflorescence a paniculate subcorymbiform compound cyme; peduncles 1.5–7 cm long, slender, sparsely tomentulose, finely scabridulous near summit; heads erect, small, about 30-flowered; involucre campanulate 6–7 mm long, about 4 mm wide at middle, sparsely tomentulose, scabridulous; outer bracts 5–6, nearly equal, about $\frac{1}{3}$ as long as inner bracts, 0.4 mm wide, linear, acute, darker at apex; inner bracts 10, unequal, innermost slightly longer, lanceolate, obtuse, darker and white-ciliate at apex, glabrous on inner face, with numerous short black glandless setae scattered over the outer face, becoming somewhat carinate and indurate but not spongy-thickened in fruit; receptacle (?); corolla about 9 mm long; ligule 1 mm wide; teeth 0.15–0.25 mm long; corolla tube 3.5 mm long, densely pubescent with short coarse papilliform or acicular hairs; anther tube 3×1 mm dis.; appendages 0.5 mm long, lanceolate, acute; filaments 0.4 mm longer; style branches 0.75 mm long, 0.1 mm wide, acute, yellow; achenes (nearly mature) dark brown, about 5 mm long, 0.5 mm wide, \pm attenuate upward, with slightly expanded pappus disk, 10-ribbed, ribs narrow, paler, finely spiculate; pappus yellowish-white, about 5 mm long, 2-seriate, setae unequal in length and width (15–33 μ wide at base), rather soft, persistent. Flowering Oct. (?) or Jan. (?); flowers golden yellow.

Belgian Congo and Uganda, apparently rare.

Known only from 2 specimens. The type had been previously identified by Fries as *C. Rueppellii* var. *centrali-africana*, along with the type of *C. Friesii* and 2 other specimens (cf. *C. Rueppellii*, m.v. 5 and 6). The second specimen differs from the type only in having the caudical leaves glabrous instead of pubescent and in the stem being wholly glabrous. Also, the florets are slightly smaller, but the only florets available on this specimen are from a small secondary head; the flower parts are similar to those of the type. The achenes are more nearly mature than in the type specimen and are similar but about 6 mm long.

Monomorphic.

Belgian Congo: north end of Lake Kivu, Kissenye, Ninagongo, plateau, lava substrate, 1800–2000 m, *Mildbrad* 1276 (B) type. **Uganda:** Kipayo and Utakapunon, grassland, hilltop, 1212 m, *Dümmer* 697 (K).

Crepis Mildbradii is closest, perhaps, to *C. Friesii*, from which it is easily distinguished by the larger dentate leaves, the more numerous smaller heads, smaller florets and flower parts, and the notably smaller brown achenes with finer ribs and

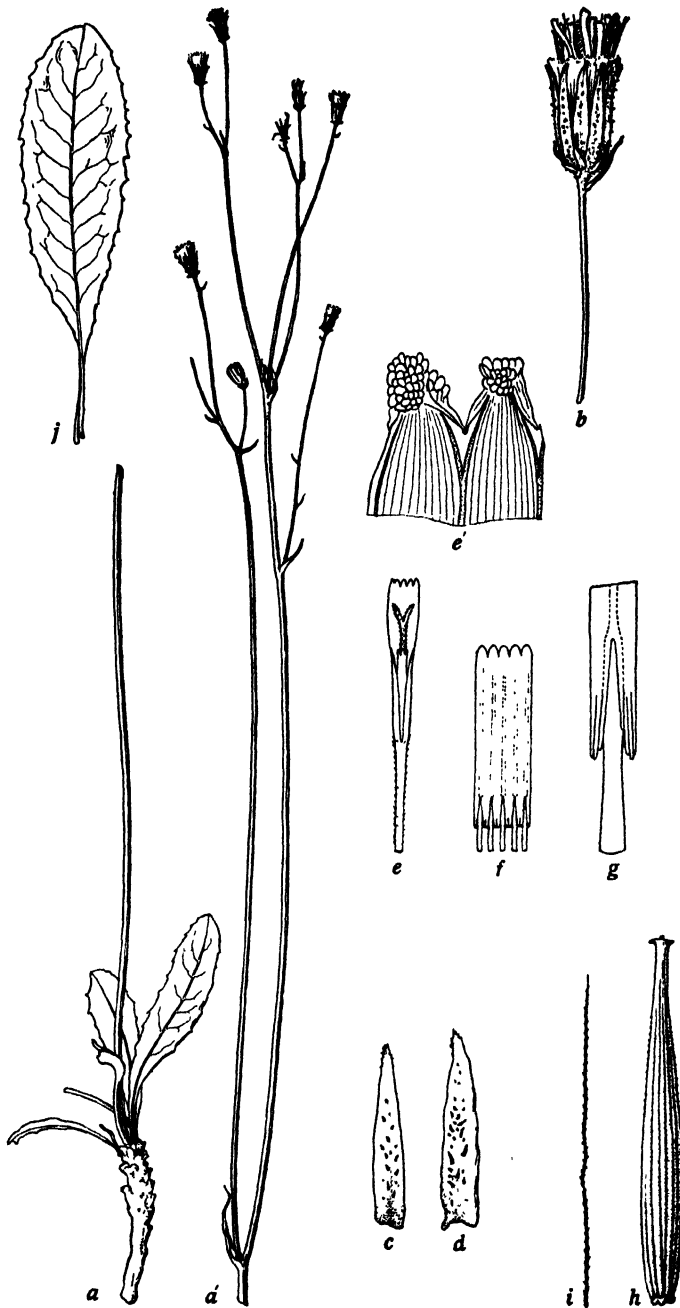


Fig. 91. *Crepis Mildbraedii*, from type (B): *a*, plant, $\times \frac{1}{2}$; *b*, flowering head, $\times 2$; *c*, *d*, inner involucre bracts from a flowering head, $\times 4$; *e*, floret lacking ovary, $\times 4$; *e'*, detail of ligule teeth, $\times 50$; *f*, anther tube, $\times 8$; *g*, detail of appendages, $\times 32$; *h*, *i*, achene and a pappus seta, $\times 8$; *j*, caudical leaf, $\times \frac{1}{2}$.

unequal pappus setae. It also shows resemblance, but less close, to *C. Newii* and *C. congoensis*. See also *C. Rueppellii*, m.v. 5 and 6. Since the pollen grains are regular, 3-pored, and 26–30 μ in diameter, this is probably a diploid species.

55. *Crepis Bruceae* sp. nov.

(Fig. 92.)

Herba perennis 1.5–3 dm alta; caudex rectus brevis 1 cm latus in radici robusto attenuatus superne foliatus; folia caudicalia ad 10 cm longa 3 cm lata oblanceolata obtusa sinuato-denticulata breve petiolata glanduloso-pubescentia; folia caulina pauca plerumque bracteiformia; caulis rectus fistulosus paululum pilosus et tenuiter glanduloso-pubescent; inflorescentia aggregata cymoso-corymbiformis; capitula parviuscula multiflora; involucria 9–10 mm longa ad basim 3–4 mm lata campanulata, squamis exterioribus 10–12 inaequalibus linearibus, interioribus circa 14 lanceolatis acutis carinatis sed in fructu non incrassatis; receptaculum nudum; corolla 9 mm longa, ligula 6 mm longa 1 mm lata flava, tubo pubescenti pilis brevis; antherae 1.6 mm longae; rami styli 0.7 mm longi flavi; achaenia nigro-fusca 4 mm longa 0.3–0.4 mm lata breve rostrata 10-costata; pappus pallido-flavidus 5 mm longus 1-seriatus persistens.

Perennial, 1.5–3 dm high; caudex vertical, short, 1 cm wide, covered with black bases of old leaves, attenuate into a strong taproot, bearing several rosette leaves and 1 or 2 stems; caudical leaves up to 10 cm long, 3 cm wide, oblanceolate, obtuse, finely sinuate-denticulate, denticles mucronate, constricted at base into a short winged petiole, midrib dark, conspicuous, finely pubescent with short brown gland hairs; stem erect, terete, striate, fistulose, \pm canescent-pilose, finely gland-pubescent, 1-branched near summit or 2-branched, the lower branch near middle, and then the first cauline leaf lanceolate, acute, closely dentate or shallowly lacinate near base, upper cauline leaves bractlike; aggregate inflorescence a few-headed corymbiform compound cyme; peduncles 0.5–2 cm long, canescent-pilose and finely gland-pubescent; heads erect, rather small, many-flowered; involucre 9–10 mm long, 3–4 mm wide near base in fruit, campanulate; outer bracts 10–12, unequal, longest $\frac{1}{2}$ as long as inner ones, linear, acuminate, \pm brown-scarious, gland-pubescent, sometimes with a few black setules near apex; inner bracts about 14, lanceolate, acute, very dark, pale membranous-margined, canescent-pilose, gland-pubescent, often with a few black glandless setules near apex, ventrally glabrous, becoming dorsally carinate enclosing marginal achenes, but merely indurate, not spongy-thickened in fruit; receptacle areolate-fimbriate, fimbriae membranous, naked; corolla 9 mm long; ligule 1 mm wide; teeth 0.2 mm long; corolla tube 2.5–3 mm long, pubescent, like base of ligule, with very short (up to 0.13 mm long) stalked acicular hairs; anther tube 1.6 \times 0.75 mm dis.; appendages 0.4 mm long, oblong, acute or obtuse; filaments unequal, 0.5–0.8 mm longer; style branches 0.6–0.8 mm long, 0.1 mm wide, attenuate, yellow; achenes (nearly mature) dark brown, 4 mm long, 0.3–0.4 mm wide, marginal slightly curved, inner straight, gradually attenuate upward into a beak 0.5–1 mm long and 0.15 mm wide, with expanded pappus disk, constricted at the narrow hollow base, with a unilateral lip or callosity, 10-ribbed, ribs equal, rounded, finely spiculate to summit; pappus yellowish-white, 5 mm long, 1-seriate, rather fine, soft, united at base, persistent. Flowering Jan.; flowers yellow.

Known only from the type locality, where it was reported as “not infrequent.”

Monomorphic.

Tanganyika: Morogoro, Uluguru Mts., Lukwangule, summit grassland, 2484 m, Miss E. M. Bruce, Jan. 30, 1935 (K, UC 557860) type, isotype.

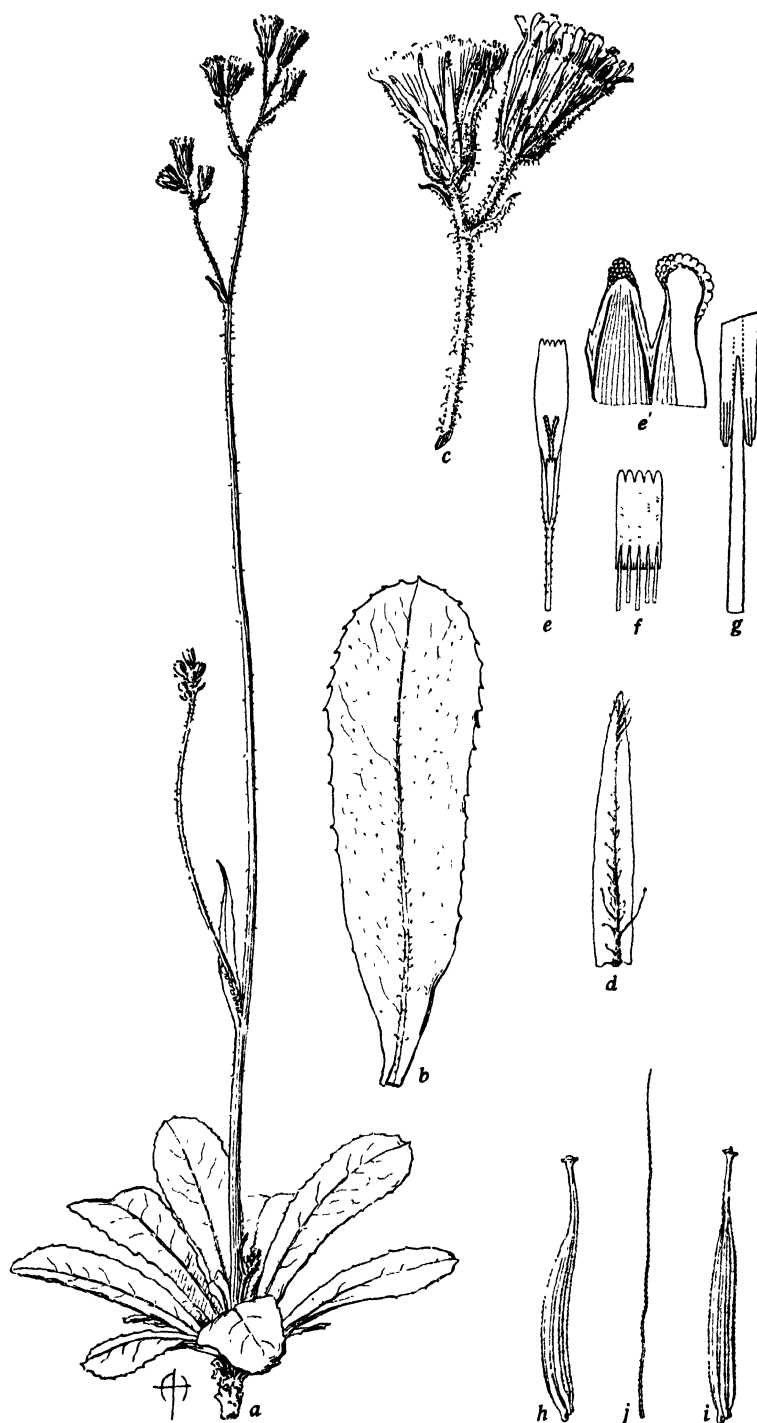


Fig. 92. *Crepis Bruceae*, from type (K) and isotype (UC 557860): *a*, plant, $\times \frac{1}{2}$; *b*, caudical leaf, $\times 1$; *c*, flowering and fruiting head, $\times 2$; *d*, inner involucre bract, $\times 4$; *e*, floret lacking ovary, $\times 4$; *e'*, detail of ligule teeth, $\times 50$; *f*, anther tube, $\times 8$; *g*, detail of appendages, $\times 32$; *h-j*, achenes and a pappus seta, $\times 8$.

Relationship

Crepis Bruceae is closely related to *C. Mildbraedii* and *C. Friesii*, as well as to *C. Newii*, but is very distinct from them in the more numerous and extremely reduced florets and achenes and in the glandular indumentum of the whole plant. Considering the small size of the fruits and flowers and the character of the aggregate inflorescence, this must be considered to be the most advanced species in this section, even though the inner involucre bracts are not spongy-thickened. Apparently the pollen grains are both 3-pored and 4-pored, which may indicate that this is some sort of polyploid.

SECTION 9. GEPHYROIDES

Relationships of the species

Two of the species in this section are perennials and the other is an annual. They are characterized by mostly glabrous leaves and stems, the stems rather low, slender, erect or (*C. leontodontoides*) semidecumbent, the involucre cylindric-campanulate, the outer bracts $\frac{1}{5}$ – $\frac{1}{3}$ or (*C. tingitana*) $\frac{1}{2}$ as long as the inner, the inner bracts becoming carinate and spongy-thickened, and similar flowers and fruits. They

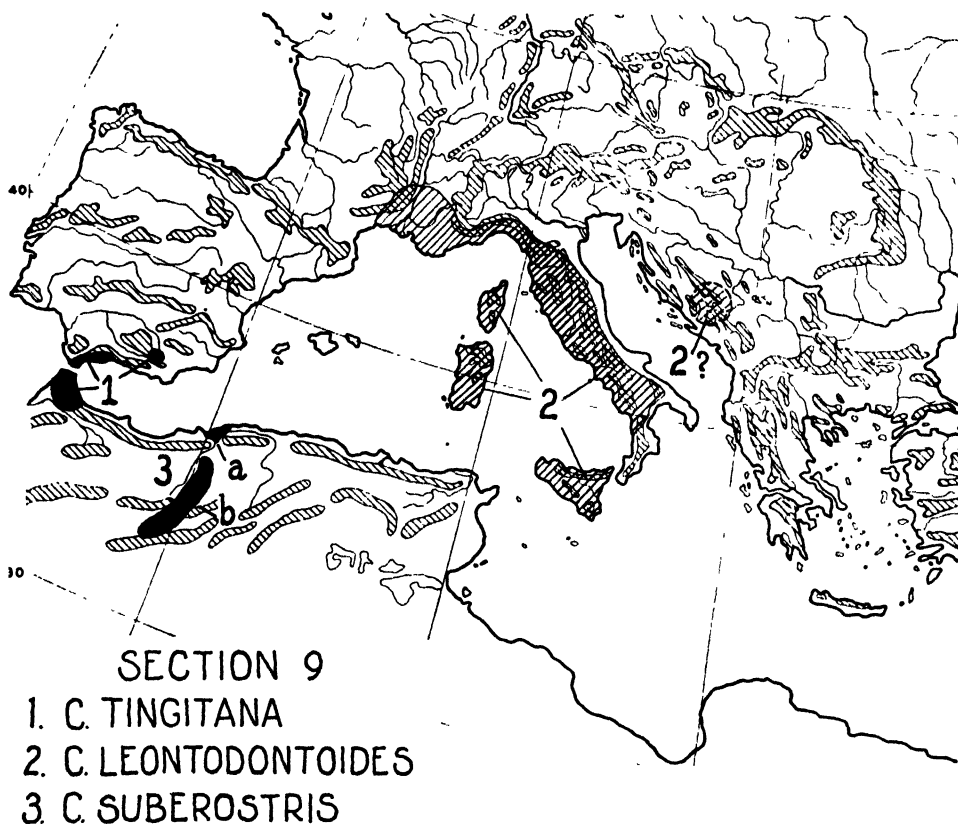


Fig. 93. Geographic distribution of the 3 species in sec. 9. Based on Goode Base Map No. 124. By permission of the University of Chicago Press.

all have 5 pairs of chromosomes, and the karyotypes are similar, except that the chromosomes are smaller in *C. leontodontoides* than in the other 2 species. On morphological grounds *C. tingitana* is certainly the most primitive of the 3 species; and it is noteworthy that its area of distribution is farthest removed from the assumed center of origin of the genus (see fig. 93). In its perennial fleshy caudex, larger dark brown achenes, and rather coarse often dusky white pappus this species shows resemblance to some of the species of tropical Africa (sec. 8). Next stands *C. leontodontoides*, also perennial, of maritime Italy and France; because of the experimental evidence (see Part I, p. 56) for its genetical relationship with *C. aurea* (sec. 4), on one hand, and with several much more advanced species, on the other, this is a very interesting species. This evidence supports the morphological indications that this section must be considered as a connecting or bridging group between more

primitive and more advanced species in the genus. *C. suberostris*, an annual of W. Algeria, is obviously close to the other 2 species, although considerably more advanced in its annual habit and smaller heads, flowers, and fruits.

Key to the Species of Section 9

- Root obconical or fusiform, fleshy; caudical leaves spatulate, the blade retrorsely dentate or lobed; heads medium or large; involucre 11–13 mm long; the outer bracts $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner56. *C. tingitana*, p. 405
- Root slender, elongated into a taproot or fibrillate; caudical leaves oblanceolate, denticulate to bipinnate; heads small or medium; involucre 7–10 mm long; outer bracts $\frac{1}{5}$ – $\frac{1}{3}$ as long as the inner.
- Plant perennial or biennial; involucre 3–4 mm wide at middle in fruiting heads, tomentulose or glabrous or rarely finely gland-pubescent; both outer and inner bracts with a medio-dorsal nerve, the inner bracts glabrous on inner face; achenes attenuate or beaked57. *C. leontodontoides*, p. 408
- Plant annual; involucre 5–8 mm wide in fruiting heads, gland-pubescent and black-setulose; outer and inner bracts without a mediodorsal nerve, the inner bracts pubescent on inner face; achenes beaked, the beak very short and coarse or longer and finer58. *C. suberostris*, p. 411

56. *Crepis tingitana* Salz.

Ex Ball, Jour. Linn. Soc. 16: 537. 1878. (Fig. 94.)

Perennial, 1.5–2.3 dm high; root obconical or fusiform, fleshy, 2–5 cm long, 0.5–0.8 cm wide, attenuate into a taproot or furcate, bearing fine fibers; caudex simple or 2–3-divided at crown; caudical leaves up to 9 cm long, 2 cm wide, spatulate, blade 2–5 cm long, elliptical, obovate or oblanceolate, rather abruptly attenuate into the long slender petiole with broader clasping base, obtuse, conspicuously retrorsely dentate, mucronate, glabrous or rarely the upper face hispidulous; cauline leaves 3–4, mostly sessile, amplexicaul, auriculate, oblanceolate or lanceolate, acute, dentate, denticulate or uppermost bractlike; stem or stems erect, simple, 1-headed, or 1–4-furcate with pedunculate branches, slender, purplish near base, green above, striate, glabrous or sparsely gland-setulose above; peduncles 2–9 cm long, not thickened at base of head, tomentulose or setulose; heads erect, medium or large, many-flowered; involucre cylindric-campanulate, 11–13 mm high, 5–6 mm wide near base in fruiting heads, canescent-tomentulose, pubescent with black glandless setules, partially reflexed at maturity; outer bracts 10–12, lanceolate, $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner; inner bracts 11–15, lanceolate, obtuse, \pm ciliate at apex, membranous-margined, dorsally keeled and spongy-thickened at maturity, ventrally pubescent with white hairs; receptacle alveolate-fimbriate, alveolae 0.3–0.4 mm wide, fimbriae 0.25 mm high, fringed with white hairs about as long; corolla 15 mm long; ligule 2.5 mm wide; teeth 0.3–0.6 mm long; corolla tube 4.5 mm long, sparsely beset with stout acicular hairs 0.1–0.3 mm long; anther tube 3.75×1 mm dis.; appendages 0.6 mm long, narrow, acute; filaments 0.75 mm longer; style branches 2 mm long, 0.1 mm wide, yellow; achenes very dark reddish-brown, 5–8 mm long, 0.5–0.8 mm wide, fusiform, strongly attenuate or coarsely beaked, paler near the expanded yellow pappus disk, abruptly attenuate to the narrow hollow base, with white calloused ring, 10-ribbed, ribs slightly rounded, finely spiculate; pappus 5–6 mm long, pure or dusky white, 2-seriate, rather coarse, stiff, persistent. Flowering Mar.–May; flowers yellow. Chromosomes, $2n = 10$.

Hieracium tingitanum Salz., in herb. 1825, ex Ball, Jour. Linn. Soc. 16: 537. 1878.

Crepis baetica [baetica] Lange, Kjoeb. Vidensk. Meddel. 227. 1877–1878.

Hieraciodes tingitanum O. Kuntze, Gen. 1: 346. 1891.

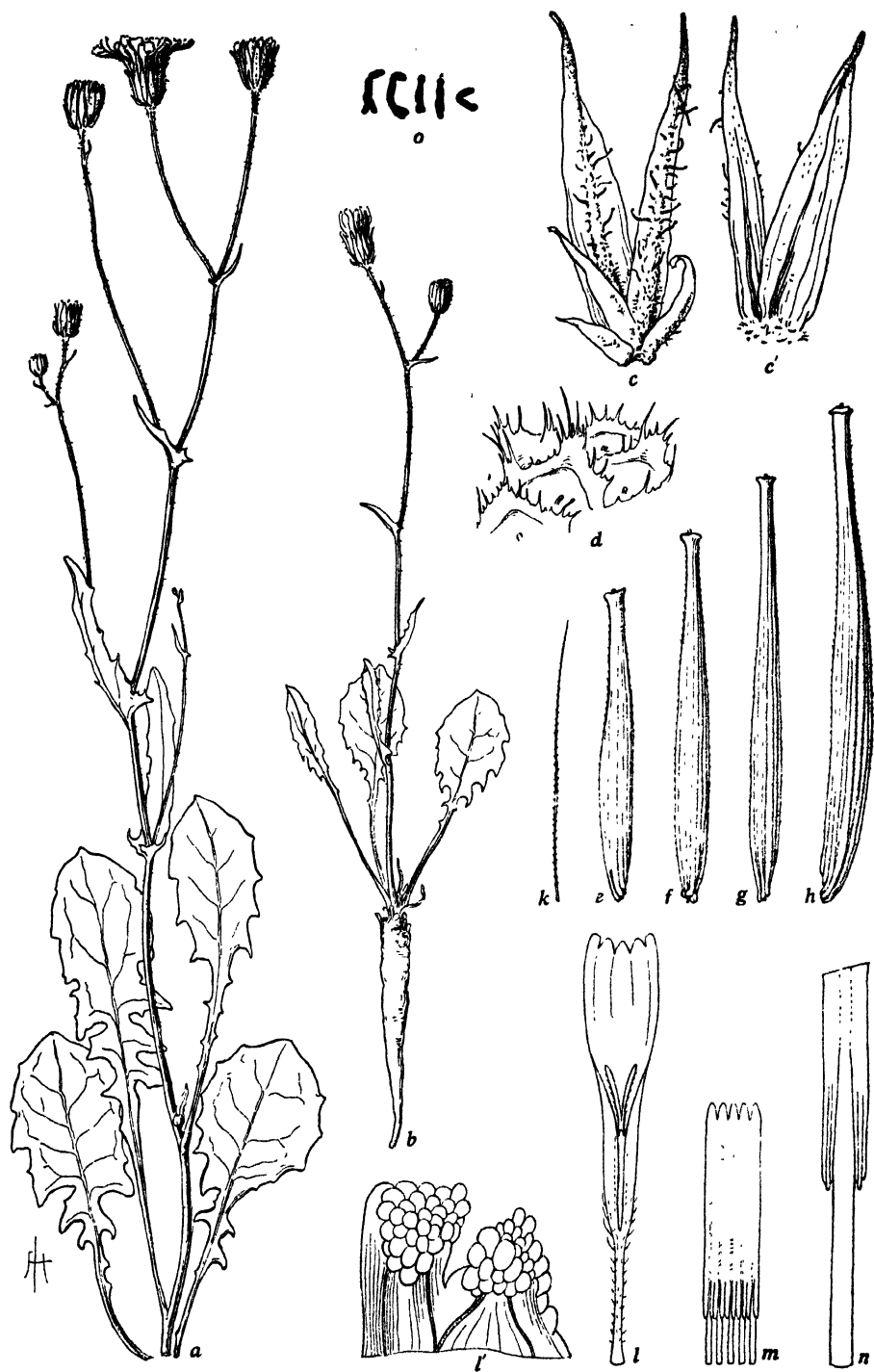


Fig. 94. *Crepis tingitana*, a, from type (K); b, from isotype (UC 295964); c-k, from Goffart in 1922 (UC 660566); l-n, from Font Quer 730 (UC 485068); o, from hort. genet. Calif. 1681 (grown from seed collected by Dr. Font Quer at the type locality for *C. baetica* Lange in Cadiz Prov., Spain): a, plant lacking caudex, $\times \frac{1}{2}$; b, plant, $\times \frac{1}{2}$; c, outer face, c', inner face of 2 adjacent involucral bracts, $\times 4$; d, detail of receptacle, $\times 25$; e-h, achenes, showing range of variation in size and shape (from wild plants, locus classicus), $\times 8$; i, floret lacking ovary, $\times 4$; l, detail of ligule teeth, $\times 50$; m, anther tube, $\times 8$; n, detail of appendages, $\times 32$; o, somatic chromosomes, $n = 5$, $\times 1250$.

The question of priority has been definitely settled, with the assistance of Professor Carl Christensen of Copenhagen, who wrote as follows: "The paper in which Lange described *C. boetica* was read for the Society [Danish Natural History Society] Feb. 15, 1878 and evidently must have been printed later in the year, while *C. tingitana* was published Feb. 27, 1878. It seems therefore sure that *C. tingitana* is the oldest published name." Although Ball transferred this species from *Hieracium* to *Crepis*, his own type specimen collected by Hooker at Casa Blanca, Morocco, in 1871, is a form of *C. amplexifolia* (Godr.) Willk. Thus, it becomes necessary to cite Salz. ex Ball.

Spanish Morocco and S.W. Spain.

Morocco, around Tangiers, is the type locality; and as the plant has been collected in that vicinity several times, even as recently as 1930, it may be assumed to be indigenous there. This assumption is strengthened by the existence of specimens from other localities in Morocco. One of Hooker's specimens is labeled "Tangier and Tetuan," and another, "Tangier to Cape Spartel." Furthermore, there is a specimen from Cape Spartel and another from "Danem Riffia," probably a locality in Er Rif. This species occurs here and there throughout a considerable area in S.W. Spain, that is, in the southern half of Cadiz, W. Malaga and N.E. Jaen. Furthermore, Willkomm (263) reports it from the mountain terraces of Granada as well as higher Andalusia. Hence, this species is certainly indigenous in Spain and almost surely indigenous in Morocco.

The type closely resembles the type of *C. baetica* Lange and other Spanish forms. In fact, the several Spanish collections exhibit comparatively few marked variations (see numbered variants). Yet it is probable that thorough field studies would reveal the existence of many other variations. The range of differences in size and shape of achenes, moreover, is remarkable in this species and provides good evidence, in connection with other morphological features and its geographical distribution, for considering it a primitive type.

A certain specimen collected at Casablanca by Hooker in 1871 was identified by J. Ball as *C. tingitana*; but it was not cited by him under *C. tingitana* Salz. This specimen is the type of *C. Balliana* (q.v.).

Morocco: Tangier, *Salzmann* (K) type; Tangier, *Salzmann* in 1825 (DC) isotype; around Tangier, in waste land, *Salzmann misit 1825* (UC 295964 ex Herb. Kew) isotype; Tangier to Cape Spartel, *Hooker* in 1871 (K); Tangier and Tetuan, *Hooker* in 1871 (Bo); near Tangier, Mt. Djebel Quebir, *Salzmann misit 1839* (Bo); near Tangier, waste land, "*classicus testis*," *Font Quer 738* iter maroccanum, 1930 (UC); Cape Spartel, *Pau* in 1921 (Bar); Er Rif (†), Danem Riffia (Huyhers), mountains, *Vidal et Lopez 70* (Bar). **Spain:** Cadiz, Jerez (=Jerez de la Frontera †), in 1876 (Genoa); Cadiz, Picacho de Alcala de los Gazules (between Medina Sidonia and Campo de Gibraltar), in woods, *Bourgeau 311* (Bo); *ibid.*, 300 m, *Font Quer* in 1925 (Bar, UC) m.v. 1; Picacho de Alcala, *Bourgeau* (DS) m.v. 1; Cadiz, Puerto Real, 50 m, among pines, *Gros* in 1925 (Bar); Cadiz, above Algeciras, among trees at base of Sierra de Palma, *Hackel* in 1876 (CM); Sierra de Palma, Mt. Carbonera, 200–300 m, *Porta et Rigo 594* (Bur); above Algeciras, in mountains, *Boissier et Reuter* in 1849 (Bo) m.v. 2; Algeciras, Sierra de la Luna (between Algeciras and Tarifa), *Fritze* in 1873 (CM); Gibraltar, corkwood crags, *Wolley-Dodd 1744* (K) m.v. 1; Malaga, Sierra de Mijas (between Coin and Marbella), northern part, semiarid hills, calcareous soil, in grass, 400–500 m, *Huter, Porta, et Rigo 359* (Bo); Eivissa, S. Joan, Torrent de la Font del Murtar, *Gros* in 1918 (Bar, UC) m.v. 3; N. Jaen, near Sierra Morena, Loma de Chiclana, Chiclana, among pines, "Pinar del Frances," *Font Quer* in 1925 (Bar, UC).

Minor Variants of *C. tingitana*

1. Leaves glandless, hispid on upper surface. *Bourgeau* (DS), Picacho de Alcala, Cadiz, Spain; *Wolley-Dodd 1744* (K), corkwood crags, Gibraltar.

2. Achenes long and more definitely beaked than in type. *Boissier et Reuter* in 1849 (Bo), mountains above Algeciras, Spain.

3. Leaves oblanceolate, obtuse or acute, coarsely runcinate or lyrate-pinnatifid, gradually attenuate into a rather short narrow petiole, hispidulous on both sides, without glands, the lower cauline leaves sometimes longer than the caudical ones and longer petioled; stem hispidulous, 2-4-furcate, the branches pedunculate or 2-3-headed; involucre 10 mm high in anthesis, canescent-tomentulose, sparsely gland-pubescent; corolla 12-14 mm long; ligule purplish on outer face; style branches yellow; achenes (immature) dark brown, strongly attenuate upward; pappus 4-5 mm long, white. *Gros* in 1918 (Bar, UC), Torrent de la Font del Murtar, S. Joan, Eivissa, Spain.

Relationship

Crepis tinigitana is a rather primitive species. In fact, it shows resemblance to *Crepis hypochaeridea* and other primitive African species in the fleshy caudex, the few-headed inflorescence, the shape of anther tube appendages, and the achene characters. But the specialized features of the involucre and the variability in degree of attenuateness of the achenes indicate its connection with the other 2 species in this section. Furthermore, one of these, *C. leontodontoides*, has been found to be genetically close to *C. aurea*. The failure of repeated attempts by Avery (135-167) to cross *C. tinigitana* with *C. leontodontoides* does not necessarily indicate absence of genetic relationship. The morphological evidence indicates that *C. tinigitana* is more primitive than the other 2 species in this section.

57. *Crepis leontodontoides* All.

Auct. Fl. Pedem. 13. 1789. (Fig. 95.)

Perennial or biennial, 1-4 dm high; caudex short, woody, 0.2-1 cm wide, usually fibrillate, sometimes elongated into a vertical woody taproot, leafy at crown; caudical leaves numerous, 3-25 (mostly 5-15) cm long, 0.5-5.5 cm wide, oblanceolate, acute or obtuse, runcinately dentate, with triangular acute teeth, or runcinate-pinnatifid, with small triangular terminal lobe and triangular to linear entire or dentate lateral lobes, or strongly bipinnately parted, or lyrate with relatively large roundish-truncate or irregularly angled terminal lobe, lateral lobes always numerous, gradually diminished into the narrowly winged petiole, sometimes shortly brown-woolly at the base, lightly canescent-tomentulose or glabrous, often pubescent with pale glandless hairs mostly along veins; lower cauline leaves similar or frequently all cauline leaves much reduced or bractlike; stems 1-8, nearly erect or semidecumbent, slender, glabrous or tomentulose or pubescent near base, remotely paniculately or dichotomously branched from below or above the middle, lower branches often elongated and 1-3-headed; peduncles 1-15 cm long, slender, erect, glabrous or tomentulose, rarely shortly and finely gland-pubescent, slightly thickened and sulcate near fruiting heads; heads erect, small, 20-40-flowered; involucre cylindric-campanulate, 7-8 mm high, 3-4 mm wide at middle in fruit, tomentulose or glabrous, rarely shortly and finely gland-pubescent; outer bracts 8-9, slightly unequal, $\frac{1}{5}$ - $\frac{1}{4}$ as long as the inner in fruiting heads, ovate to lance-linear, acute or acuminate, like inner bracts rounded at the apex, the median dorsal nerve becoming narrowly carinate, yellow and spongy-thickened at base in fruit; inner bracts 9-13, lanceolate, acute, glabrous on inner face, the pale median dorsal nerve becoming narrowly carinate, yellow and spongy-thickened near base in fruit, ultimately reflexed; receptacle areolate, glabrous; corolla about 9 mm long; ligule 1.5 mm wide; teeth 0.2-0.3 mm long; corolla tube 2.5 mm long, pubescent with acicular hairs 0.05-0.2 mm long; anther tube 2.5×1 mm dis.; appendages 0.5 mm long, lanceolate, acuminate; style branches 1.25 mm long, 0.1 mm wide, yellow or green; achenes brown, yellowish at apex, 3.5-5 mm long, 0.4-0.6 mm wide, terete or subterete, gradually or strongly attenuate to the summit or with a coarse or fine beak 1-1.5 mm long, pappus disk expanded, narrowed to the finely calloused hollow

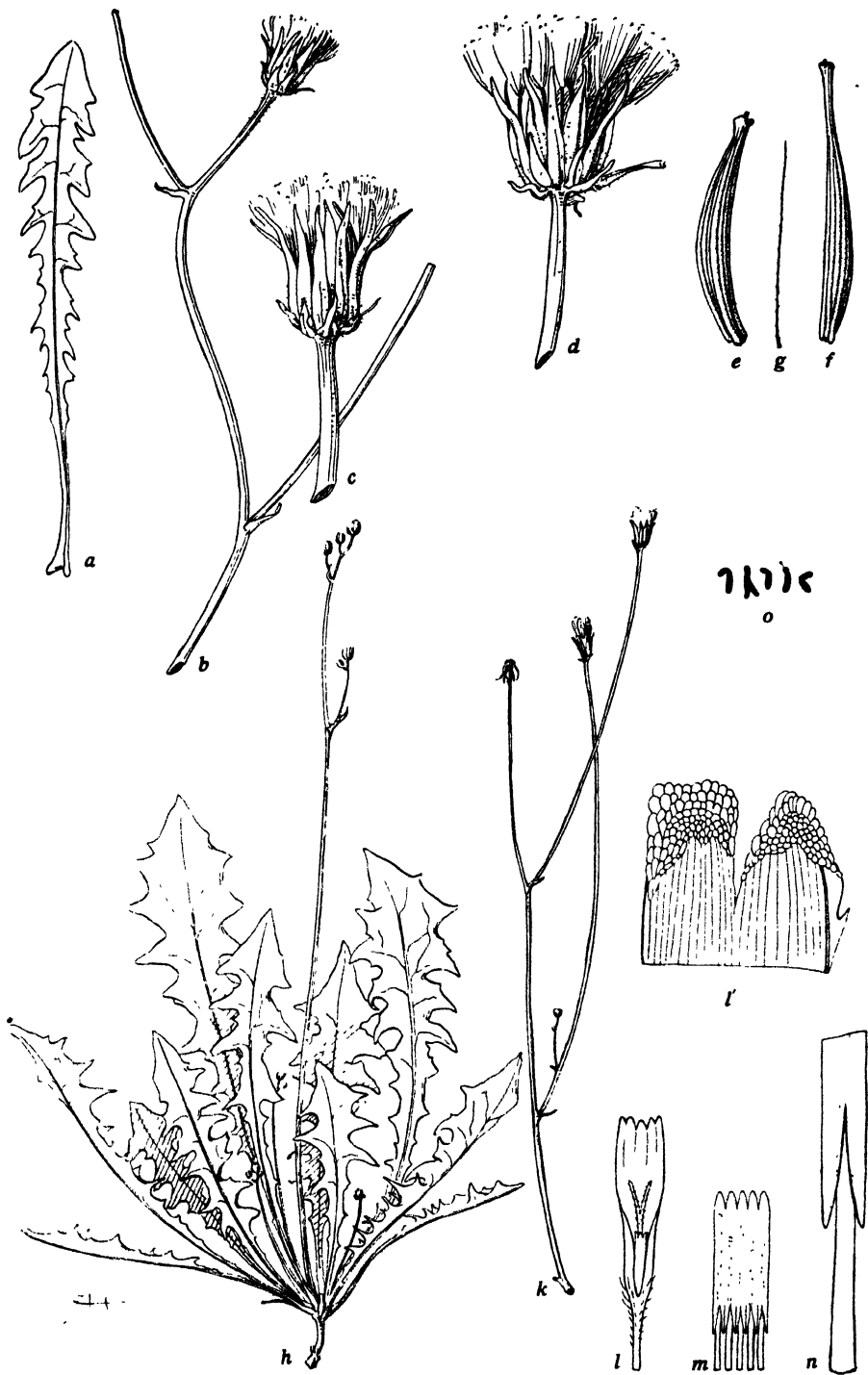


Fig. 95. *Crepis leontodontoides*, a-g, from type (Torino); h-n, from hort. genet. Calif. 28.2095 (UC 506831); o, from hort. genet. Calif. 1807 (grown from seeds received from Dr. O. Mattirola, Torino Bot. Gard.): a, caudical leaf, $\times \frac{1}{2}$; b, fragment of inflorescence, $\times 1$; c, immature head, $\times 2$; d, mature head, $\times 2$; e-g, 2 achenes and a pappus seta, $\times 8$; h, plant, $\times \frac{1}{2}$; k, stem with 3 heads, $\times \frac{1}{2}$; l, floret lacking ovary, $\times 4$; l', detail of ligule teeth, $\times 50$; m, anther tube, $\times 8$; n, detail of appendages, $\times 32$; o, somatic chromosomes, $n = 5$, $\times 1250$.

base, 10-ribbed, ribs about equal, sometimes with a few weak additional striae, mucriculate or finely spiculate near apex; pappus white, 3-4 mm long, 1-2-seriate, setae very fine (about 16μ wide at base), soft, deciduous. Flowering Apr.-Aug.; flowers yellow, with or without reddish-purple on outer face of ligules. Chromosomes, $2n = 10$.

Barkhausia leontodon DC., Fl. Fr. ed. 3, 4: 43, n. 2950. 1805.

Crepis pauciflora Desf., Tabl. ed. 1, 88. 1804; ed. 2, 103. 1815 nom. nud.; Hort. Par. ex Poir., Encycl. Suppl. 2: 390-391. 1811.

Lagoseris leontodontoides Link, Enum. Hort. Berol. 2: 289. 1822.

B. nuda Presl, Del. Prag. 112. 1822.

C. triangula Presl, Del. Prag. 110. 1822; Fl. Sic. 31. 1826.

B. leontodontoides Spreng., Syst. 3: 653. 1826.

C. aetnensis Presl, Fl. Sic. 1: 31. 1826.

B. tenerima Tenore, Ind. Sem. H. R. Neapol. 14. 1830; DC., Prod. 7: 159. 1838.

B. taraxacifolia Tenore, Syll. 404. 1831, non DC.

Prenanthes Negretti Req. (Cat. Toulon, 115, *fide* Rouy, Fl. Fr. 9: 216. 1905) et ex DC., Prod. 7: 156. 1838.

Hieraciodes leontodontodes O. Kuntze, Gen. 1: 346. 1891.

Apargia magellensis Tenore, ex Fiori, Fl. Anal. Ital. 3(2): 433. 1904.

Throughout most of maritime Italy, especially in the W. part—Piedmont, Liguria, Emilia, Etrusca, Toscana, Campania, S. Apennines, Apulia, Sicily, Sardinia, Corsica, and smaller islands off the coast of Italy; and S. France from Provence to Cevennes; Dalmatia (adventive ?). Often found in grass among shrubs or trees, especially in dry situations; sometimes on rocks and walls. It has been reported from elevations between 900 and 1700 m in the S. Apennines.

Highly variable in size of plant (extremely reduced variants occur), in degree of dissection of the leaves, and in shape and position of the lobes, in nature and amount of indumentum on leaves and involucre, as well as in degree of attenuateness of the achenes. In view of this variability the extensive synonymy of the species is not surprising; nor is the recognition of a number of varieties by various authors (cf. DC., *loc. cit.*; Fiori, *loc. cit.*; Rouy, *loc. cit.*). The recognition of these varieties, even as minor variants, would seem to call for the recognition of many more equally distinct forms. In general, these variations occur throughout the range of the species. An exception to this may be a form with gland-pubescent involucre and peduncles (var. *Preslii Nicotra* Fiori) which is known only from Sicily and S. Italy.

The following critical specimens have been seen by me: the type in Herb. Allioni, Torino (photograph in Herb. Univ. Calif.); authentic specimens of *Prenanthes Negretti*, *Barkhausia nuda* and *C. pauciflora* in Herb. DC. Prod.; and *P. Negretti* in Herb. Requien, Avignon. Many specimens were seen in the rich collection of the Herbarium at Firenze which are not cited below.

Italy: Piedmont, Monteferrato (Torino, UCf) type; Etrusca, Maggio in 1836 (SF); S. Liguria, Apuane Alps, J. Ball in 1862, 1866 (Mo, G); Tuscana, Elba, Gulfo Stella, Sommier in 1900 (Ms); Campania, Rome, Griayon in 1856 (Rome), Ischia, Gussone (Naples); Camaldoli, near Naples, Guadagnom in 1920 (US); Apennines of Pistoria, J. Ball in 1844 (US); Apulia, Gargano, Porta et Rigo 342 (UC); Apulia, Mons Garganus, beechwoods near "la Casa forestale," 850 m, Fiori in 1913, Fiori et Bég., Fl. It. Exs. 2190 (Bur, G) as var. *Preslii Nicotra* fa. *villosa*; Sicily, Stromboli, Gussone in 1828 (UC); Sicily, Syracuse, Avola, Rigo 73 (Bur); Sicily, Messina, Ross 557 (Bur). **France:** Corsica, Cap Corse, Mobile 246 (K); Corsica, near Zonza, dry hillside along Zonza R., about 700 m, Babcock 366a (UC); Iles d'Hyères, Legré in 1895 (Ms); Ile du Porquerolles, dry pine woods, Raine in 1907 (G); Marseille, Montredon, Jordan (DS); Marseille, Reynier (Po); Var, near Toulon, Metz in 1869 (Ms).

Relationship

Crepis leontodontoides finds its nearest relatives in this section, although its chromosomes are all smaller in size than those of the other 2 species. It also exhibits considerable resemblance in habit, leaves, heads, flowers, and fruits to *C. bellidifolia*, a 4-paired species occurring in the same region. The crossing experiments of Avery (135–167), involving *C. leontodontoides* as one parent, revealed its genetic relationship with such a primitive species as *C. aurea* and such advanced species as *C. tectorum*, *C. parviflora*, *C. capillaris*, and *C. Marshallii* (see Part I, p. 56). These are additional reasons for considering this section as a bridging group, connecting the more primitive and most advanced sections of the genus.

58. *Crepis suberostris* Coss. et Durieu

Ex Batt. et Trab., Fl. de l'Alger, 561. 1888–1889. (Figs. 96, 97.)

Annual, 0.8–3.8 dm high; root slender; caudex \pm swollen, simple or \pm divided, 1–6-stemmed, leafy; caudical leaves 2–12 cm long, 1–2 cm wide, oblanceolate, obtuse or acute, denticulate to pinnately or bipinnately lobed or divided, glabrous or obscurely pubescent; cauline leaves similar or lanceolate, sessile, acutely auriculate, amplexicaul, uppermost bractlike; stem erect, usually branched from near base, branches strict or arcuate, the lower elongated, 2–6-headed, glabrous or scabridulous, in depauperate forms stem very slender, 1–3-headed; peduncles 1–10 cm long, slender, gland-pubescent or glabrescent; heads erect, medium to small, many-flowered; involucre cylindric-campanulate, 7–10 mm long, 5–8 mm wide at middle in fruit, gland-pubescent, intermixed with black glandless setules; outer bracts 8–10, linear, $\frac{1}{4}$ – $\frac{1}{3}$ as long as the inner and paler; inner bracts about 12, lanceolate, acute, ventrally pubescent with white or yellowish shining hairs, dorsally carinate and spongy-thickened confluent with base of involucre in fruit; receptacle areolate, shortly and finely ciliate; corolla 10–11 mm long; ligule 1.1–1.4 mm wide; teeth 0.25 mm long; corolla tube 2.25–3 mm long, pubescent with acicular hairs up to 0.8 mm long; anther tube 2.5–3.2 mm long; appendages 0.5–0.6 mm long, narrow, acute; filaments very short; style branches 1.25–1.5 mm long, yellow; achenes brown, 2.3–4 mm long, very shortly and coarsely beaked or the beak about $\frac{1}{4}$ as long as the whole achene and much finer, constricted at the narrow white-calloused base, the small pappus disk white, 10-ribbed, ribs narrow, rounded, smooth or muriculate; pappus white or whitish, 4–5 mm long, scarcely exceeding the involucre.

Algeria, the Oran littoral, and in the interior from the lower uplands to the high arid plateaus.

Two subspecies are recognized. The one on which the species was based occurs in the littoral region, whereas the other, which has heretofore been recognized as a species, is found in the interior. Another form, an intermediate one, has been collected by the author between this littoral region and the interior, but no plants typical of either subspecies were found here. Although very similar in general morphology, the subspecies are distinct in certain characters and they are extremely different ecologically.

Key to the Subspecies of *Crepis suberostris*

- Lower leaves mostly pinnate or bipinnate (sometimes dentate or denticulate in small specimens); achenes 2.3–3 mm long, dark brown, with a very short coarse beak; pappus pure white, about 4 mm long; plants of Oran littoral58, *a. typica*
- Lower leaves denticulate (rarely dentate or shallowly lobed); achenes 3–4 mm long, pale brown, with a slender beak about $\frac{1}{4}$ as long as the whole achene; pappus dusky white, about 5 mm long; plants of Oran uplands58, *b. arenaria*



Fig. 96. *Crepis suberostris typica*, a, e-j, from Babcock 244 (UC 429541); b-d, from isotype, Balansa 197 (Fl): a, plant, $\times \frac{1}{2}$; b, fruiting head, $\times 2$; c, d, achene and pappus seta, $\times 8$; e, floret lacking ovary, $\times 4$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, old head, $\times 2$; i, somatic chromosomes, $n = 5$, $\times 1250$; j, detail of receptacle, $\times 25$.

58, *a. Crepis suberostris typica* subsp. nov. Folia caudicalia plerumque pinna-tifida; capitula paululum parvior; involucria pallidior saepe tomentulosa; antherae 2.5 mm longae; achaenia nigro-fusca 2–3 mm longa, rostro brevissimo et crasso; pappus niveus 4 mm longus uniseriatus.

Caudical and lower cauline leaves glabrous, mostly pinnately lobed or divided, the lobes often dentate, sometimes with narrow secondary lobes, sometimes, in de-pauperate plants, dentate or denticulate; heads slightly smaller; involucries paler, often canescent-tomentulose; anther tubes shorter and wider, $(2.5)3 \times$ about 1 mm dis.; achenes 2.3–3 mm long, dark brown, abruptly attenuate into the very short coarse beak; pappus pure white, about 4 mm long, 1-seriate, very fine, soft, caducous. Flowering Mar.–May. Chromosomes, $2n = 10$. See fig. 96.

Barkhausia suberostris Coss. et Durieu in sched.

Dunes and sandy wastes near the shore of the Mediterranean in the vicinity of Mostaganem, Oran Prov., Algeria.

Regarding the type of this subspecies, Battandier and Trabut cite no specimens in their description; hence it is necessary to designate a certain specimen. The first two collections cited below are both authentic. But the second (Balansa, no. 197), represented in several herbaria and having the printed label bearing the name *Barkhausia suberostris* DR. ined., is hereby designated as the type collection and the plant attached to the printed label in the general harbarium at Paris is accepted as the type (photograph in Herb. Univ. Calif.).

Algeria: Oran Prov., environs of Mostaganem, *Delestre* in 1847 (P, PC ex hb. Sch. Bip.); Mostaganem, in sandy places, *Balansa* 197 (type P, UCf, K, Fl, Ms) isotypes; Oran, dunes at the bridge of La Macta, *Cosson* in 1875 (K); Oran, Dahra dist. (east of Mostaganem), toward the river mouth of Oued Khamis (= Kramis †), *Cosson* in 1875 (P); La Macta, near Mostaganem, coastal sands, *Faure* in 1915, 1930, 1933, 1934 (UC, G); La Macta, $1\frac{1}{2}$ km east of railway station, S. side of dunes near route to Mostaganem, *Babcock* 244, 245 (UC); between Mostaganem and Mascara, 6 km south of Akoubir, sandy waste along route, *Babcock* 246 (UC) m.v. 1.

Minor Variant of C. suberostris typica

1. Plant more divaricate, as in some forms of subsp. *arenaria*; leaves denticulate to runcinate-pinnatifid; achenes 2.7–3.7 mm long, gradually attenuate into a short rather coarse beak. The achenes are actually intermediate between those of the subspecies; and in leaves and habit this form is also intermediate. Although 3 plants were collected at the station named below, the extent of the distribution of this variant was not determined. No plants typical of either subspecies were seen in this vicinity. This form may be an ecotype rather than of hybrid origin. *Babcock* 246 (UC) 6 km south of Akoubir, route from Mostaganem to Mascara, Algeria.

58, *b. Crepis suberostris arenaria* (Pomel) comb. nov. Caudical and lower cauline leaves pubescent with very fine short hairs or glabrescent, mostly denticulate, rarely dentate or shallowly lobed; heads slightly larger; involucries darker, \pm tomentulose, the thin tomentum usually yellowish; anther tubes longer and narrower, 3.2×0.7 mm dis.; achenes 3–4 mm long, light brown, gradually attenuate into a fine beak about $\frac{1}{4}$ as long as the whole achene; pappus dusky white, about 5 mm long, 2-seriate, fine, soft, caducous. Flowering Apr.–May. See fig. 97.

Crepis arenaria Pomel, Nouv. Mat. Fl. Atl., 261. 1874 nota, et ex Batt. et Trab., Fl. Alg., 562. 1888–1890.

Oran Prov., Algeria, in the interior, uplands and lower highlands, including arid plateaus.

Algeria: Oran Prov., high arid plateau, Itima, *Pomel* in 1860 (type Alger, isotypes UC); Mascara, *Durieu* in 1844 (P) 5 specimens, 3 of which are on same sheet with type of subsp. *typica*, photographs of these and of the other 2 specimens (UC); Mascara, sandy lawns, *Warion* in 1872 (K, US, Ms, Fl, Alger, UC); Cheddad, high plateau, *Battandier* (Alger, UC); Ain-Sefra, moun-tains of S. Oran, in sand, *Battandier* in 1906 (Alger, UC).

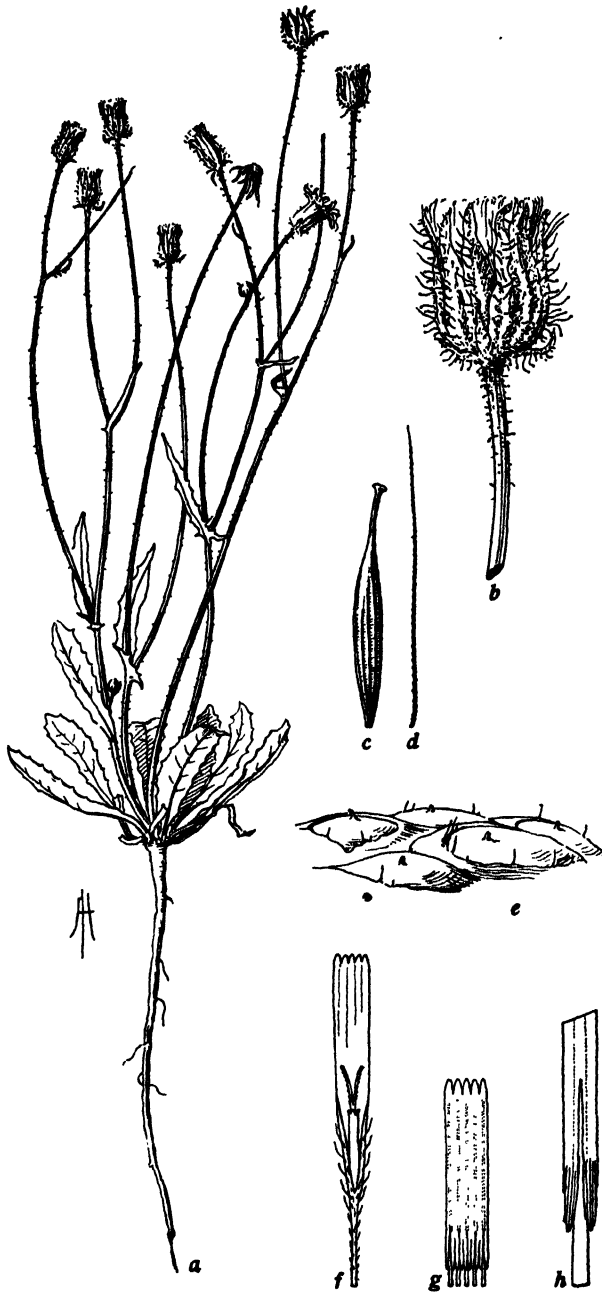


Fig. 97. *Crepis suberostris arenaria*, from isotype (UC 313834): a, plant, $\times \frac{1}{2}$; b, fruiting head, $\times 2$; c, d, achene and pappus seta, $\times 8$; e, detail of receptacle, $\times 25$; f, floret lacking ovary, $\times 4$; g, anther tube, $\times 8$; h, detail of appendages, $\times 32$.

Relationship

Crepis suberostris has as its nearest relatives the two 5-paired species, *C. tingitana* and *C. leontodontoides*. In karyotype, *C. suberostris* resembles *C. tingitana* more than *C. leontodontoides*. But in leaves, flowers, and fruits it is much more like the latter and crosses with *C. leontodontoides* have produced sterile hybrids. In size of the flowers and fruits it is more reduced than either of the other species. This reduction and its annual habit indicate that it is a more advanced species than the other 2.

SECTION 10. BERINIA

Relationships of the Species

The 29 species of this section are characterized by the woody perennial root elongated into a taproot, the usually simple caudex bearing 1 or several stems, the caudical leaves oblanceolate or sometimes elliptic or linear, the cauline leaves more or less reduced, the heads mostly large or medium, with numerous florets, the involucre campanulate, with the longest outer bracts $\frac{1}{4}$ – $\frac{3}{4}$ as long as the inner and the inner bracts becoming more or less modified by thickening, the achenes unbeaked or rarely with a short coarse beak and with 10–30 ribs or striae, and the pappus usually white.

The species of this section fall into 4 subsections on the basis, primarily, of size and habit of the plant and, secondarily, of leaf width and degree of reduction of the cauline leaves. Subsection C, **Corymbiformae**, contains 11 species which are characteristically tall plants, each with numerous large leaves, a robust stem, and several branches forming a corymbiform or sometimes a racemiform inflorescence. These 11 species may be segregated into 4 subgroups: (1) *C. Strausii*, *C. darvasica*, *C. songorica*, *C. sonchifolia*; (2) *C. ciliata*, *C. biennis*; (3) *C. pannonica*, *C. latialis*, *C. bertisceae*, *C. chondrilloides*; (4) *C. bupleurifolia*.

(1) The 4 species of the first subgroup, on the basis of size of heads, florets and achenes, and the shape and ribbing of the achenes, are the most primitive in the whole section **Berinia**. They are little known species and, from the few collections thus far made, they appear to be local endemics, the first in W. Persia, the next two in Turkestan, and the fourth in the E. Caucasus (see fig. 98). Although they have not been examined cytologically, the chromosome numbers determined for a few of the species in this section indicate that they have either 5 or 4 pairs.

(2) The 2 species in the second subgroup both have about 40 chromosomes in their somatic cells and have been shown (B. and Sw., 236, 265) to be octoploids with the base number 5. Their distribution is strikingly different. *C. ciliata* is known only from a few localities in the S. Caucasus reg.; whereas *C. biennis*, one of the best-known species in the genus, occurs from E. Russia to middle Spain and northward as far as the Baltic states, S. Sweden and Norway, and the British Isles. A possible explanation of this remarkable difference in distribution in 2 somewhat related though very distinct high polyploids is suggested in the text under the species in question. Morphologically these 2 species approach the first subgroup in degree of primitiveness, especially in head size and in the long outer bracts, although the achenes are not so primitive in type.

(3) The 4 species in the third subgroup are closely interrelated and they, too, have an interesting distribution. *C. pannonica*, the most primitive, extends from the Caspian reg. westward through N. Persia, the Caucasus, and S. Russia to the N. Balkans and Istria, where it reaches the restricted areas of the endemics, *C. bertisceae* and *C. chondrilloides*. *C. latialis* is also endemic, being found only in middle and S. Italy. Thus, we find the most primitive member of this subgroup extending from the region of the assumed center of origin of the genus to the region where its 3 close relatives occur as endemics. Of these 4 species, only *C. bertisceae* has not been examined cytologically; the other 3 have $n=4$ chromosomes and closely similar karyotypes.

(4) The fourth subgroup consists of *C. bupleurifolia*, with its 2 subspecies, *typica* and *meletonis*. It is not closely related to any species in the entire section, but it shows more similarity to the other members of this subsection than to any of the

other subsections. It is known from only 2 localities in W. Kurdistan and 1 in W. Armenia; and it has not been studied cytologically.

Subsection D, **Subcorymbiformae**, contains 5 species which are characterized by stature lower than that of those in the preceding section, rather large lower leaves, furcate stems, with a few ascending branches forming a subcorymbiform inflorescence, small, mostly bractlike, cauline leaves, and usually few flower heads. There are 3 subgroups: (1) *C. auriculaefolia*; (2) *C. Baldaccii*, *C. turcica*, *C. Pantocsekii*; (3) *C. Triasii*.

(1) *C. auriculaefolia*, because of its very unequally ribbed achenes and its distribution as a local endemic in Crete, may be considered the most ancient species in this subsection. Although its involucre is more specialized, by thickening of the bracts, than that of *C. Baldaccii*, this may have developed under the influence of a more xerophytic environment. *C. auriculaefolia* shows more resemblance in leaves and achenes to *C. Raulini*, also of Crete, and in leaves and habit to *C. Triasii* of the Balearics, than to the other species in this subsection. This also indicates the greater antiquity of *C. auriculaefolia*. Although it has not been examined cytologically, it, like *C. Raulini*, probably has 5 pairs of chromosomes, but the karyotype may be more primitive than in *C. Raulini*.

(2) *C. Baldaccii*, *C. turcica*, and *C. Pantocsekii* have a strong general resemblance in size and habit of the plant but differ in many details. *C. Baldaccii* is certainly the most primitive in head size and width and length of the bracts. It has 5 pairs of chromosomes and a primitive karyotype, somewhat resembling that of *C. pontana*. The other 2 species have not been examined cytologically.

(3) *C. Triasii*, with its highly specialized involucre and shortly beaked achenes, is a much more advanced species than *C. auriculaefolia* or *C. Baldaccii*, and it has only 4 pairs of chromosomes. However, the morphological evidence of genetic relationship of *C. Triasii* with *C. auriculaefolia* and *C. Raulini* is marked, and these 3 species would provide valuable material for a cytogenetic investigation.

Subsection E, **Divaricatae**, contains 9 species which are characterized by low stature of the plant, rather large lower leaves, slender furcate stems with spreading branches, small cauline leaves, and a few flower heads. There are 6 subgroups: (1) *C. Raulini*; (2) *C. albanica*, *C. macropus*; (3) *C. oporinoides*; (4) *C. dens-leonis*; (5) *C. Sibthorpiana*, *C. khorassanica*; (6) *C. incana*, *C. taygetica*.

(1) *C. Raulini*, on the basis of head size, bract length, and achene type, is the most primitive species in this subsection. It exhibits strong similarities to *C. auriculaefolia* in its leaves, involucre, and achenes. It has 5 pairs of chromosomes, but a less primitive karyotype than that of *C. Baldaccii*. Although generally similar, it does not exhibit close affinity with the other species in this subsection.

(2) *C. albanica* happens to show more resemblance, especially in habit, to *C. macropus* of Asia Minor than is found in the Balkan species of subsection D. It is evident, however, that there is a fairly close connection between *C. macropus* and these 4 Balkan species. Neither *C. albanica* nor *C. macropus* has been examined cytologically.

(3) *C. oporinoides* of the Sierra Nevada in S. Spain exhibits some resemblances to *C. biennis* of subsection C, and there is some basis (see p. 474) for thinking that it is related to the 5-paired ancestral species from which *C. biennis*, through polyploidy, was derived, although *C. oporinoides* has only 4 pairs of chromosomes. Its classification in this subsection, being on the basis of size and habit, emphasizes the close relationships within the whole section.

(4) *C. dens-leonis* is a very little-known species of the Caucasus (see p. 476). Apparently it is fairly close to the preceding species of this subsection.

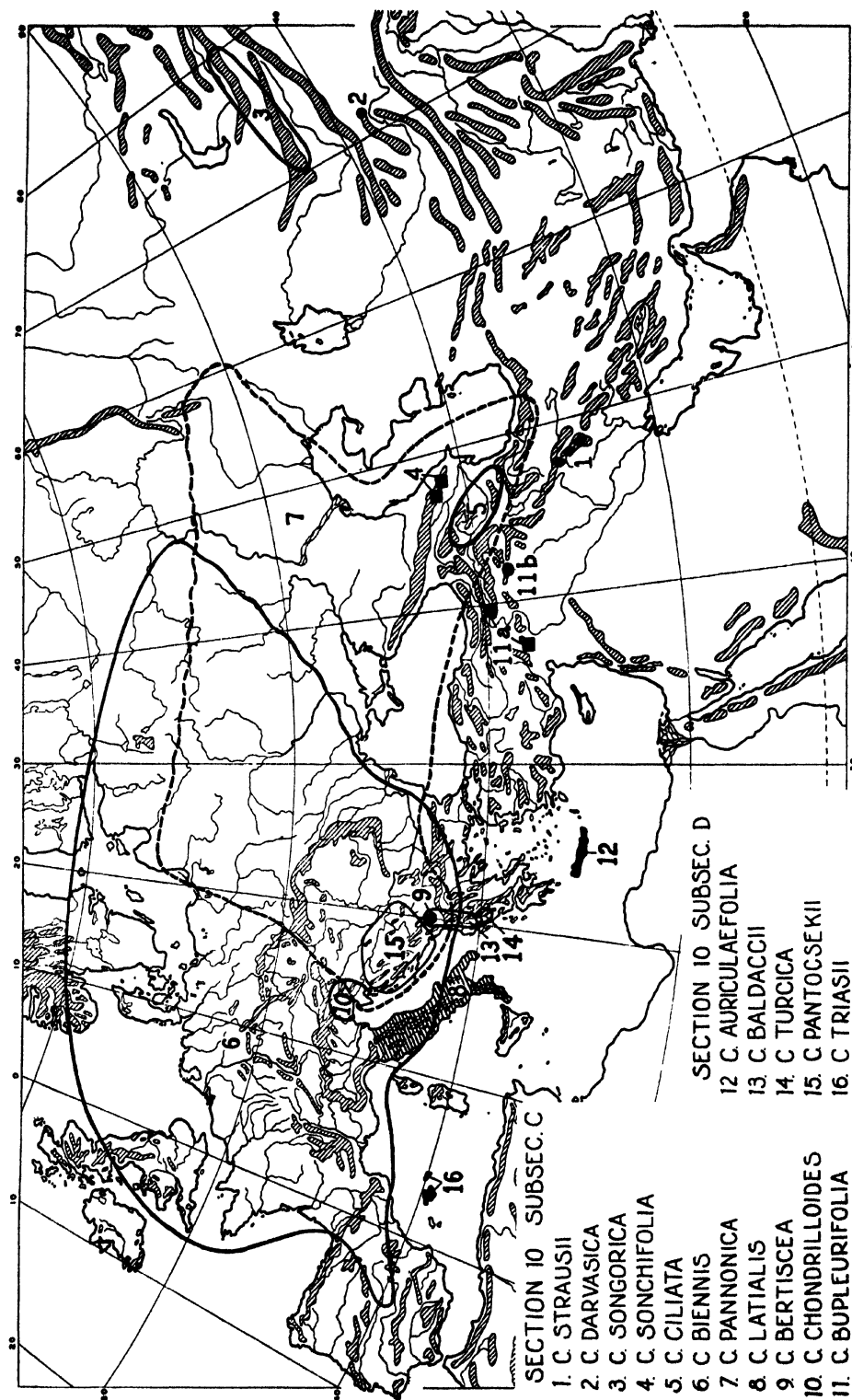


Fig. 98. Geographic distribution of the species in sec. 10, subsections C and D. The numerous narrow areas shaded with single diagonal lines represent mountain ranges or groups. Single stations are shown by solid circles, 2 known stations by solid squares, and 3 known stations by solid diamonds. Based on Goode *Base Map No. 124*. By permission of the University of Chicago Press.

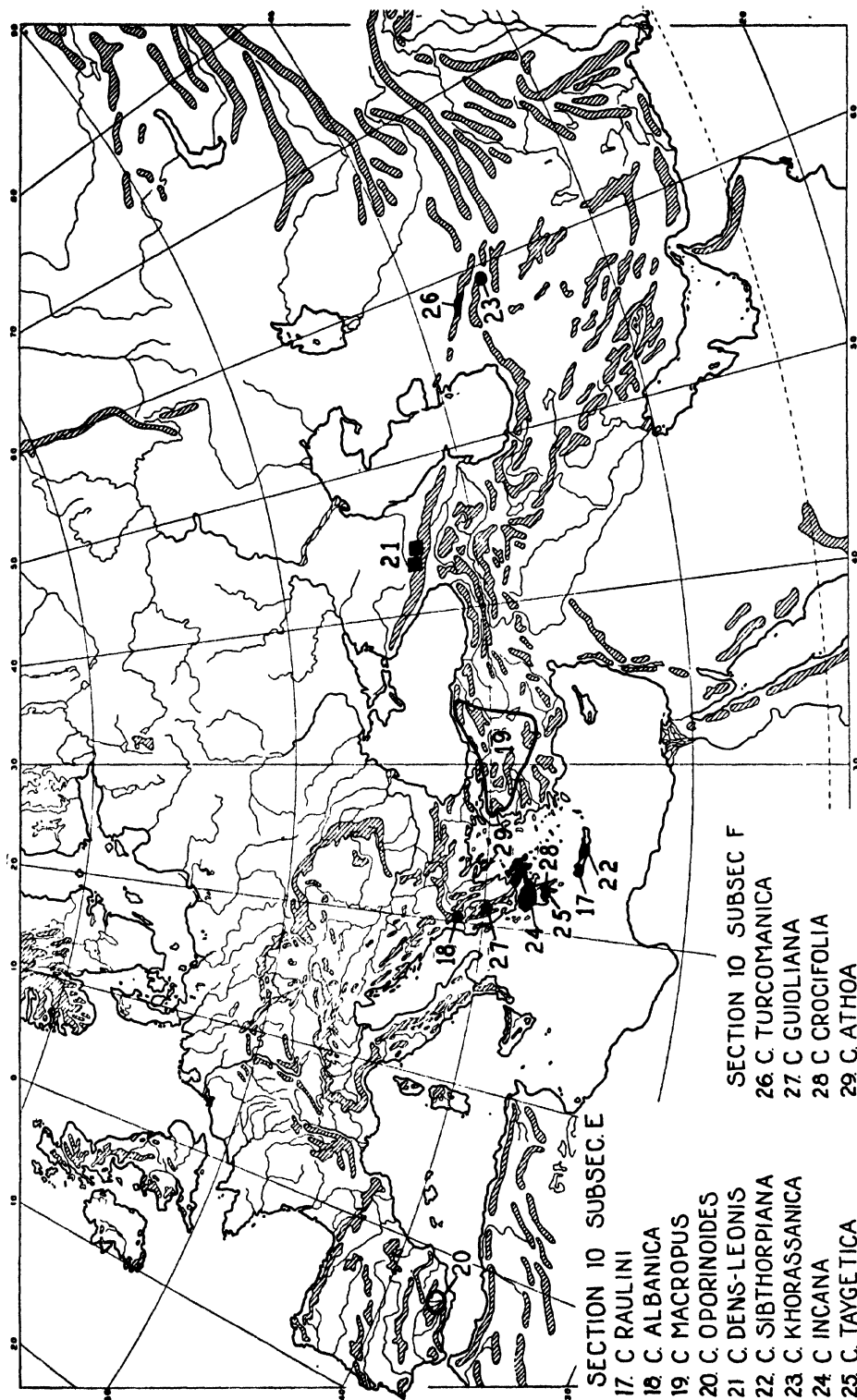


Fig. 99. Geographic distribution of the species in sec. 10, subsections E and F. The numerous narrow areas shaded with single diagonal lines represent mountain ranges or groups. Single stations are shown by solid circles, 2 known stations by solid squares. Based on Goode *Base Map No. 124*. By permission of the University of Chicago Press.

(5) *C. Sibthorpiana*, an endemic in Crete, and *C. khorassanica*, which is known from only 1 locality in north-central Persia, are certainly closely related. The former is considerably more reduced in size of plant, heads, bracts, and florets than *C. Raulini*, and the achenes have only 10 equal ribs. Yet the two are obviously related. From what little is known about *C. khorassanica*, it seems to be a distinct species.

(6) *C. incana* and *C. taygetica*, both of S. Greece, are generally similar, although very distinct in number of florets per head, size of florets, and especially in color of the ligules. *C. incana* has 16 chromosomes in its somatic cells, and *C. taygetica* has about 40; hence, both are polyploid; the base number in *C. incana* is 4 and in *C. taygetica* it is probably 5.

Subsection F, **Strictae**, contains 4 species which are characterized by narrow leaves and low, slender, few-branched stems, the branches being elongated and strictly erect. *C. turcomanica* and *C. Guioliana* are about equally primitive with respect to involucre and achenes, but the former has larger florets. *C. crocifolia* and *C. athoa* are considerably more reduced throughout. The first 2 species are known from only 1 or 2 collections, and they may be very local endemics. The other 2 are certainly local endemics. *C. turcomanica* occurs in S.W. Turkestan and the other 3 are found in Greece.

Considering the distribution of the whole section, **Berinia** (figs. 98, 99), we find that it extends from Spain to Turkestan in the general zone of the 40th parallel of north longitude, with some northward extension of the 2 widespread species, *C. pannonica* and *C. biennis*. But many of the species are endemic relics which are scattered over the range of the section. The distribution as a whole, therefore, is wholly consistent with the concept that the center of origin for the genus was in Central Asia.

Key to the Subsections and Species of Section 10

- A Plants taller, 2–12 (mostly 3–6) dm high; stem robust, always stronger than the branches, with several cauline leaves approaching the caudical ones in size, lanceolate or elliptic Subsection C. **CORYMBIFORMAE**
- B Outer involucre bracts long, mostly $\frac{1}{2}$ – $\frac{3}{4}$ as long as the inner; inner bracts densely pubescent on inner face.
- C Cauline leaves narrow at the base, not auriculate-amplexicaul; involucre often setulose, with short setules on inner bracts only; corolla tube pubescent, with 2–3-celled acicular trichomes 64. *C. biennis*, p. 435
- CC Cauline leaves broad at the base, auriculate-amplexicaul; involucre densely setose, with yellowish setae on both outer and inner bracts; corolla tube pubescent, with short papilliform trichomes 63. *C. ciliata*, p. 432
- BB Outer involucre bracts shorter, mostly $\frac{1}{4}$ – $\frac{1}{2}$ as long as the inner; inner bracts glabrous or sometimes sparsely pubescent near the apex on inner face.
- D Cauline leaves, at least the middle ones, auriculate or rounded at the base, amplexicaul.
- E Caudical and lower cauline leaves merely denticulate or dentate, not pinnatifid.
- F Inner involucre bracts not darker at the apex, but with a darker median nerve, often setose, with coarse fleshy setae; corolla tube strigulose, with stout setiform many-celled scales 59. *C. Strausii*, p. 424
- FF Inner involucre bracts darker at the apex, but without a darker median nerve or, if a black median line is present (*C. sonchifolia*), then not coarsely setose; corolla tube pubescent, with short hairs.
- G Leaves closely dentate; peduncles stout, rigid, sulcate; heads 50–90-flowered; achenes 5–6 mm long 65. *C. pannonica*, p. 439
- GG Leaves remotely denticulate or dentate; peduncles slender, arcuate; heads 30–40-flowered; achenes 6–8 mm long.
- H Plant 5–6.5 dm high; outer involucre bracts linear, glabrescent; corolla about 21 mm long, the tube 9–10 mm long; achenes orange-colored, 6–7 mm long, 16–18-ribbed. 60. *C. darvasica*, p. 426
- HH Plant 2–4 dm high; outer involucre bracts lanceolate; glandular; corolla about 17 mm long, the tube 6 mm long; achenes reddish-brown, 8 mm long, 12–15-ribbed 61. *C. songorica*, p. 426
- EE Caudical and lower cauline leaves lyrate-pinnatifid.
- I Lateral segments of the leaves numerous, close; middle and upper cauline leaves acutely auriculate; mature involucre 7–9 mm wide at middle; achenes 13–18 ribbed, the ribs nearly equal 67. *C. bertisceae*, p. 446
- II Lateral segments of the leaves few, remote; middle and upper cauline leaves rounded at the base; mature involucre 3–5 mm wide at middle; achenes 5-costate, each costa striate or 3-ribbed 69. *C. bupleurifolia*, p. 451
- DD Cauline leaves neither auriculate nor rounded at the base, not amplexicaul.
- J Peduncles yellow-tuberculate at the base; corolla about 20 mm long, the ligule 15 mm long, 2.5 mm wide; anther tube 7 mm long; achenes 7 mm long 62. *C. sonchifolia*, p. 429
- JJ Peduncles not tuberculate at the base; corolla 13–15 mm long, the ligule (9)10 × 2 mm; anther tube 4–5 mm long; achenes 4.5–7 mm long.
- K Principal leaves pinnatifid or bipinnatifid, with 5–7 pairs of lateral segments; heads 40–50-flowered; involucre 8–11 mm long 66. *C. latialis*, p. 444
- KK Principal leaves pinnately divided to the narrow rachis into very numerous close linear or filamentous segments; heads 50–75-flowered; involucre 11–14 mm long 68. *C. chondrilloides*, p. 448

AA Plants shorter, 0.6–4.7 (mostly 1–3.5) dm high; stem more slender, often little stronger than the branches, with few or no cauline leaves approaching the caudical ones in size, or if with several such, then the cauline leaves linear.

L Caudical leaves broader, 1–5 (mostly 2–4) cm wide, oblanceolate; branches divaricate, or if mostly strict (subsection D), then inflorescence paniculate or subcorymbiform.

M Branches mostly strict; inflorescence paniculate or subcorymbiform Subsection D. **SUBCORYMBIFORMAE**

N Inner involucre bracts strigulose or finely pubescent on inner face; achenes \pm attenuate but not definitely beaked.

O Leaves saliently dentate; inner bracts densely strigulose on inner face; receptacle long-ciliate 70. **C. auriculaefolia**, p. 454

OO Leaves runcinate-pinnatifid or pinnately lobed; inner bracts finely pubescent on inner face; receptacle shortly ciliate.

P Involucre gland-pubescent; longest outer bracts $\frac{3}{8}$ – $\frac{3}{4}$ as long as the inner.

Q Leaves coarsely dentate or shallowly pinnatifid; inner involucre bracts silky-pubescent on both faces toward the apex; achenes with every fourth or fifth rib stronger .. 71. **C. Baldaccii**, p. 457

QQ Leaves deeply pinnatifid, with narrow dentate segments; inner involucre bracts pubescent on inner face; achenes with the ribs nearly equal 73. **C. Pantocsekii**, p. 461

PP Involucre densely tomentose, not gland-pubescent; longest outer bracts $\frac{1}{2}$ as long as the inner 72. **C. turcica**, p. 459

NN Inner involucre bracts glabrous on inner face; achenes definitely though shortly beaked 74. **C. Triassii**, p. 463

MM Branches divaricate; inflorescence diffusely spreading Subsection E. **DIVARICATAE**

R Inner involucre bracts pubescent or strigulose on inner face.

S Heads 30–80-flowered; involucre with 12–20 inner bracts.

T Involucres gland-pubescent; ligules yellow, without red on outer face; achenes grayish-tawny or reddish-brown; pappus white.

U Caudical leaves 3–8 cm long, denticulate to coarsely runcinate-dentate; involucre yellowish- or brownish-green; corolla in marginal florets about 14 mm long; achenes unequally ribbed ... 75. **C. Raulini**, p. 466

UU Caudical leaves 10–15 cm long, deeply and irregularly runcinate-pinnatifid or lyrate; involucre very pale at the base, with dark bracts; corolla in marginal florets about 18 mm long; achenes nearly equally ribbed 76. **C. albanica**, p. 468

TT Involucres not gland-pubescent; ligules reddish-purple on outer face; achenes yellowish; pappus pale yellowish 78. **C. oporinoides**, p. 472

SS Heads about 20-flowered; involucre with 8–10 involucre bracts.

V Leaves runcinately dentate or pinnatifid, with triangular segments; inner involucre bracts canescent-tomentose, not setulose on outer face, pubescent on inner face; pappus white, 5 mm long 80. **C. Sibthorpiana**, p. 476

VV Leaves retrorsely dentate; inner involucre bracts dark green, with a yellow median line and short stout setules, strigulose on inner face; pappus yellow-white, 7 mm long 81. **C. khorassanica**, p. 477

RR Inner involucre bracts glabrous on inner face.

W Plant 2.2–3.5 dm high; flower heads about 50-flowered; inner involucre bracts 12–16.

X Longest outer involucre bracts $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner; achenes reddish-brown, 7 mm long, 10-ribbed77. *C. macropus*, p. 470

XX Longest outer involucre bracts $\frac{1}{4}$ as long as the inner; achenes dark brownish-purple, 5 mm long, 18–20-ribbed.....79. *C. dens-leonis*, p. 474

WW Plant 0.3–1.5 dm high; flower heads 15–40-flowered; inner involucre bracts 10.

Y Flowers magenta pink; heads 30–40-flowered; pappus 8 mm long82. *C. incana*, p. 479

YY Flowers yellow, with red stripe on outer face of ligule; heads about 15-flowered; pappus 6 mm long83. *C. taygetica*, p. 481

LL Caudical leaves narrower, 0.2–3 (mostly 0.5–2) cm wide, linear or narrowly oblanceolate; branches strictly or arcuately erectSubsection F. **STRIOTAE**

Z Outer involucre bracts 5–6; inner bracts shortly pubescent on outer face; florets about 21 mm long; receptacle densely ciliate, with yellow hairs84. *C. turcomanica*, p. 483

ZZ Outer involucre bracts 8–12; inner bracts glabrous or tomentose on outer face; florets 12–14 mm long; receptacle glabrous or white-ciliate.

a Heads 30–40-flowered; outer bracts $\frac{1}{2}$ – $\frac{2}{3}$ as long as the inner; inner bracts 12–16, pubescent on inner face.

b Achenes 7–10 mm long, about 1 mm wide, 16–20-ribbed; pappus 5–7 mm long ...85. *C. Gujoliana*, p. 485

bb Achenes 4–5 mm long, 0.5 mm wide, 16-striate; pappus 4.5–5.5 mm long87. *C. athoa*, p. 489

aa Heads 11–14-flowered; outer bracts $\frac{1}{3}$ as long as the inner; inner bracts 9–10, glabrous on inner face86. *C. crocifolia*, p. 487

SUBSECTION C. CORYMBIFORMAE

59. *Crepis Strausii* Bornm.

Beih. Bot. Centralbl. 32: 416. 1914. (Fig. 100.)

Perennial, about 3 dm high, mostly glabrous, except the heads; caudex 1 cm wide, divided, crowning a strong vertical taproot; caudical leaves 10–18 cm long, 2–3 cm wide, runcinate-pinnatifid, terminal lobe oblong, obtuse, subentire, lateral lobes triangular, acute, attenuate into a narrowly winged petiole, with prominent pale midrib, sometimes sparsely puberulent beneath or the margin hairy; lower and middle cauline leaves oblong, broadly auriculate-amplexicaul, coarsely triangular-dentate, acute, the uppermost leaves reduced, bractlike; stems rather stout, dichotomously branched from below the middle, terete, striate; branches long, pedunculate or furcate, 2-headed; peduncles long, arcuate, gradually thickened upward, bracteate, like involucre farinose-canescens; heads large, many-flowered; involucre 12–15 mm long, 7–9 mm wide at middle in fruiting heads; outer bracts about 12, unequal, the longest $\frac{1}{2}$ as long as inner bracts, narrow, appressed or spreading; inner bracts about 15, lanceolate, obtuse, white-ciliate at apex, pale green, the median nerve darker, becoming thickened and pale near base and often sparsely or densely beset with broad fleshy yellow or brown setae, glabrous on inner face; corolla 20 mm long; ligule 3.5 mm wide, teeth 0.4–0.8 mm long, doubly gland-crested; corolla tube 5 mm long, strigulose near summit with stout acicular-tipped setiform scales 0.1–0.7 mm long; anther tube 5.75×1.5 mm; appendages 1 mm long, oblong, acute; filaments 0.75 mm longer; style branches 2.75 mm long, 0.25 mm wide, pale yellow; mature achenes (not seen, ex descr.) attenuate, not beaked, glabrous; pappus white, 6 mm long, 2–3-seriate, fine, soft. Flowering May–June; flowers yellow.

Monomorphic.

W. Persia: Kermanschah, Mt. Kuh-i-Parrau, Nudschuheran Pass, *Th. Strauss* in 1906 (Bornm) type; *ibid.*, Teng-i-Dinawer, *Strauss* in 1904 (Bornm); Mt. Schahu, *Strauss* in 1909 (MW, Bornm, UCf).

Relationship

Crepis Strausii is obviously a little-known species. A photograph of the type is filed in the University of California Herbarium and the drawings in fig. 100 are based on this photograph and a few fragments from another specimen. Although mature achenes have not been seen, the present author could detect no indication whatever in the immature achenes of a tendency to develop a beak. The original author places this species next to *C. auriculaefolia* and *C. sonchifolia*. In habit, however, notably in the long branches and peduncles and the well-developed cauline leaves, in the setaceous involucre, and especially in the large florets with many-celled setiform trichomes on the corolla-tube, and the large anther tubes and style branches, this species shows much more resemblance to *C. sonchifolia*. Therefore, pending further information regarding its achenes and its chromosomes, and on the basis of head size, length of outer involucreal bracts, and the slight thickening of the inner bracts at maturity, it is placed provisionally as the most primitive species in this section. Although the florets are not as long as those of *C. darvasica*, they are broader and the peculiar trichomes of the corolla tube are unique.

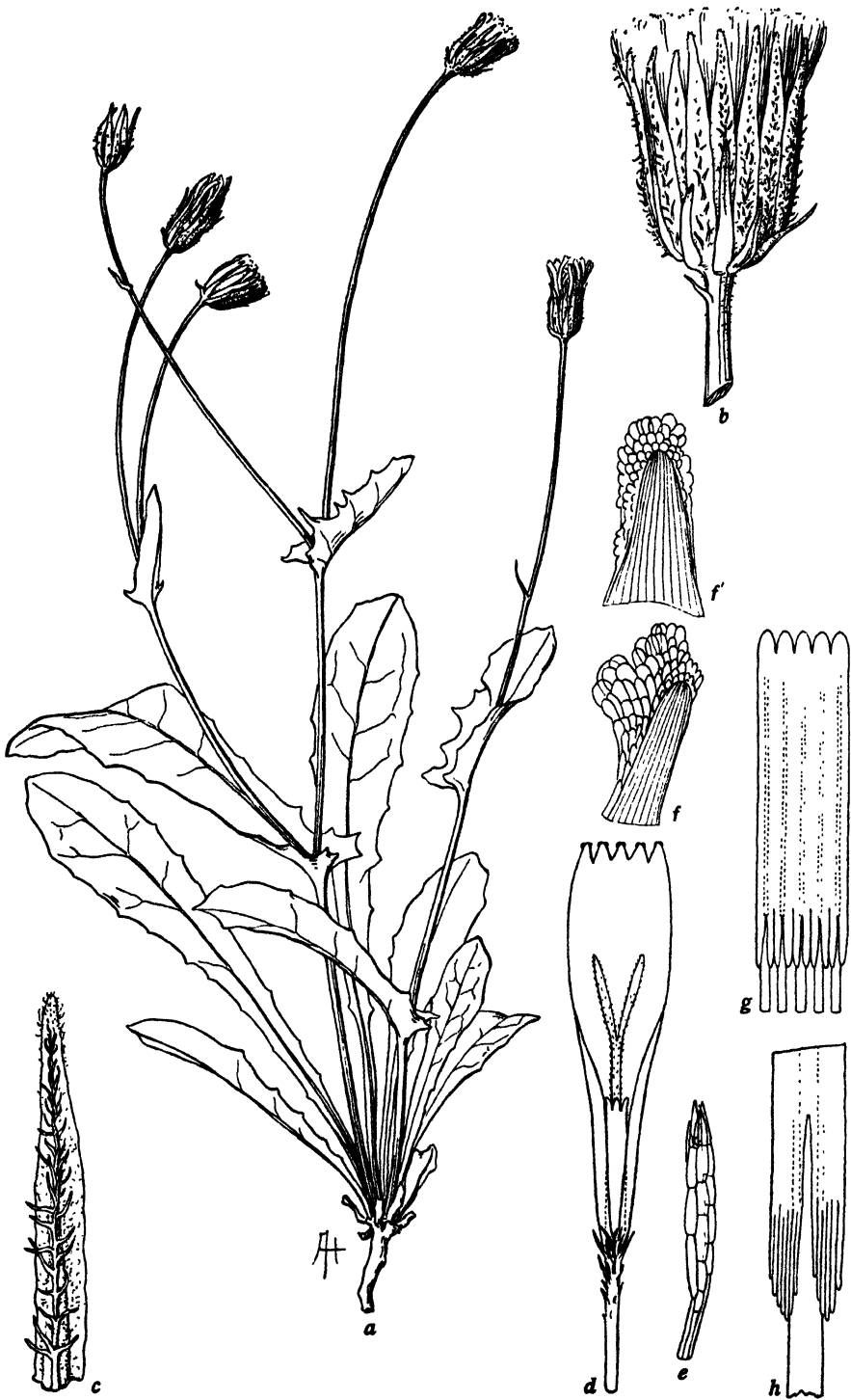


Fig. 100. *Crepis Strausii*, from Strauss in 1906 and 1909 (Bornm): a, plant, $\times \frac{1}{2}$; b, head, $\times 2$; c, inner bract, outer face, $\times 4$; d, floret lacking ovary, $\times 4$; e, setula from corolla tube, $\times 50$; f, f', details of ligule teeth, $\times 25$; g, anther tube, $\times 8$; h, detail of appendages, $\times 32$.

60. *Crepis darvasica* H. Krasch.

Acta Inst. Bot. Acad. Sci. U. S. S. R. ser. I, 1: 182. 1933. (Fig. 101.)

Perennial, 5–6.5 dm high; caudex 2–3 cm long or longer, about 1 cm wide, covered with bases of old leaves; caudical leaves 18 cm long, 3–4 cm wide, oblanceolate, acute, undulate, erose, or irregularly dentate, the teeth sometimes corneous-mucronate, gradually attenuate into a short winged petiole, strongly veined, glabrous above, pubescent on lower face with rigid hairs; cauline leaves 6–14 cm long, 4–6 cm wide, ovate to lanceolate, acute or acuminate, sessile, amplexicaul, sometimes in nearly opposite pairs, only the extremely uppermost at bases of peduncles bractlike; stems 1 or 2, erect, robust, sulcate, glabrous above, sparsely pubescent below, cymosely 3–5-branched above, aggregate inflorescence corymbiform, few-headed; peduncles 0.5–4 cm long, arcuate, \pm canescent-tomentose near the head; heads erect, medium, 30–40-flowered; involucre campanulate, 13–16 mm long, about 7 mm wide at middle in fruit, canescent-tomentose, gland-pubescent with short pale hairs and brown glands; outer bracts about 8, unequal, $\frac{1}{4}$ – $\frac{1}{3}$ as long as the inner, linear, glabrescent and dark at the apex; inner bracts about 14, lanceolate, obtuse or acute, glabrescent and dark at the apex, scarious at margin, glabrous on inner face, becoming dorsally carinate and brownish spongy-thickened at the base at full maturity; receptacle ?; corolla about 21 mm long; ligule about 3 mm wide; teeth 0.5 mm long; corolla tube 9–10 mm long, pubescent with short (0.05 mm) stout 2-celled trichomes and sometimes a few longer several-celled trichomes near the summit; anther tube 5×1.5 mm dis.; appendages 0.8 mm long, oblong, sagittate; style branches 2 mm long, 0.2 mm wide, obtuse; achenes xanthine orange (Ridgway, 13i) in color, yellowish near the summit, 6–7 mm long, 1 mm wide, fusiform, attenuate to both ends, with very slightly expanded pappus disk, abruptly narrowed at the calloused base, 16–18-ribbed, with several ribs stronger, ribs rounded, muriculate under lens; pappus white, 8–9 mm long, 4-seriate, united into a ring at the base and breaking away in clumps, unequal in length and width, the coarsest about 80μ (7 cells) wide at the base, rather soft, persistent. Flowering July; flowers yellow.

Known only from Darwaz (Darvas), a mountainous reg. in E. Bucharā (Bokhara), Russian Turkestan. The lowest and highest elevations given in Stieler's Atlas are 1300 and 3900 m, respectively.

The above description is based on an authentic specimen.

Monomorphic.

Tadzhikistania: Darvas, a place called Chobu, *Lipsky*, July 8, 1897 (Lenin, Ucf).

Relationship

The close relationship of *Crepis darvasica* to *C. pannonica* is pointed out by Krashenninikov (*loc. cit.*). It is, however, more closely similar to *C. Strausii*, *C. songorica*, and *C. sonchifolia*, from all of which it is very distinct in the unusually long corolla tube and in other details of the flowers and fruits.

61. *Crepis songorica* (Kar. et Kir.) comb. nov.

(Fig. 102.)

Perennial, 2.3–3.8 dm high; caudex straight, slender, the crown covered with brown bases of old petioles; caudical leaves oblanceolate, acute or obtuse, attenuate into a winged petiole with broader membranous clasping base, denticulate or dentate, teeth corneous-mucronate, retrorse, glaucescent, \pm hispidulous especially on midrib; cauline leaves similar, sessile, amplexicaul, the base rounded and entire,

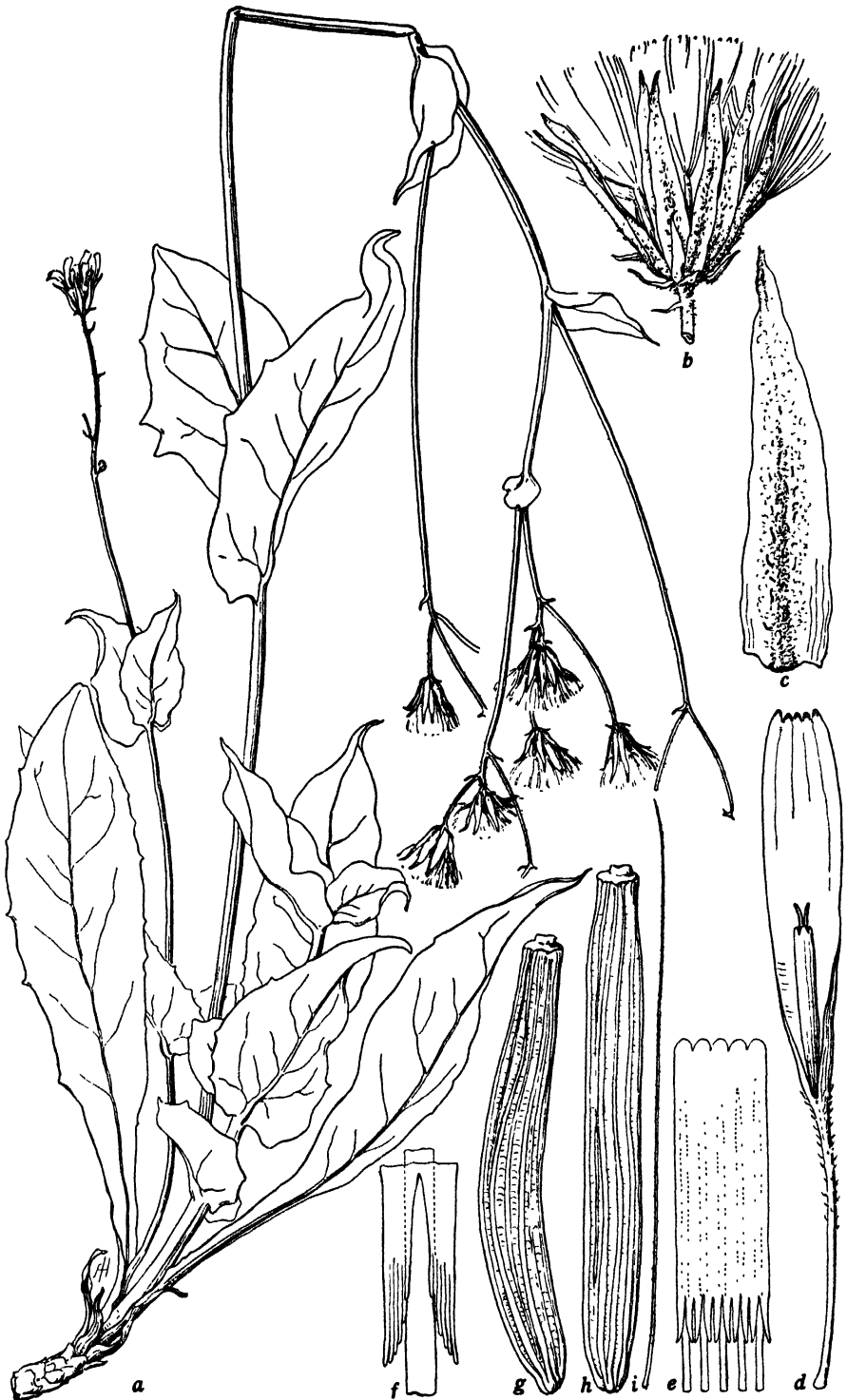


Fig. 101. *Crepis darvasica*, from *Lipsky* in 1897 (Lenin), authentic: a, plant, $\times \frac{1}{2}$; b, nearly mature head, $\times 2$; c, inner involucre bract, dorsal face, $\times 4$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g-i, 2 achenes and a pappus seta, $\times 8$.

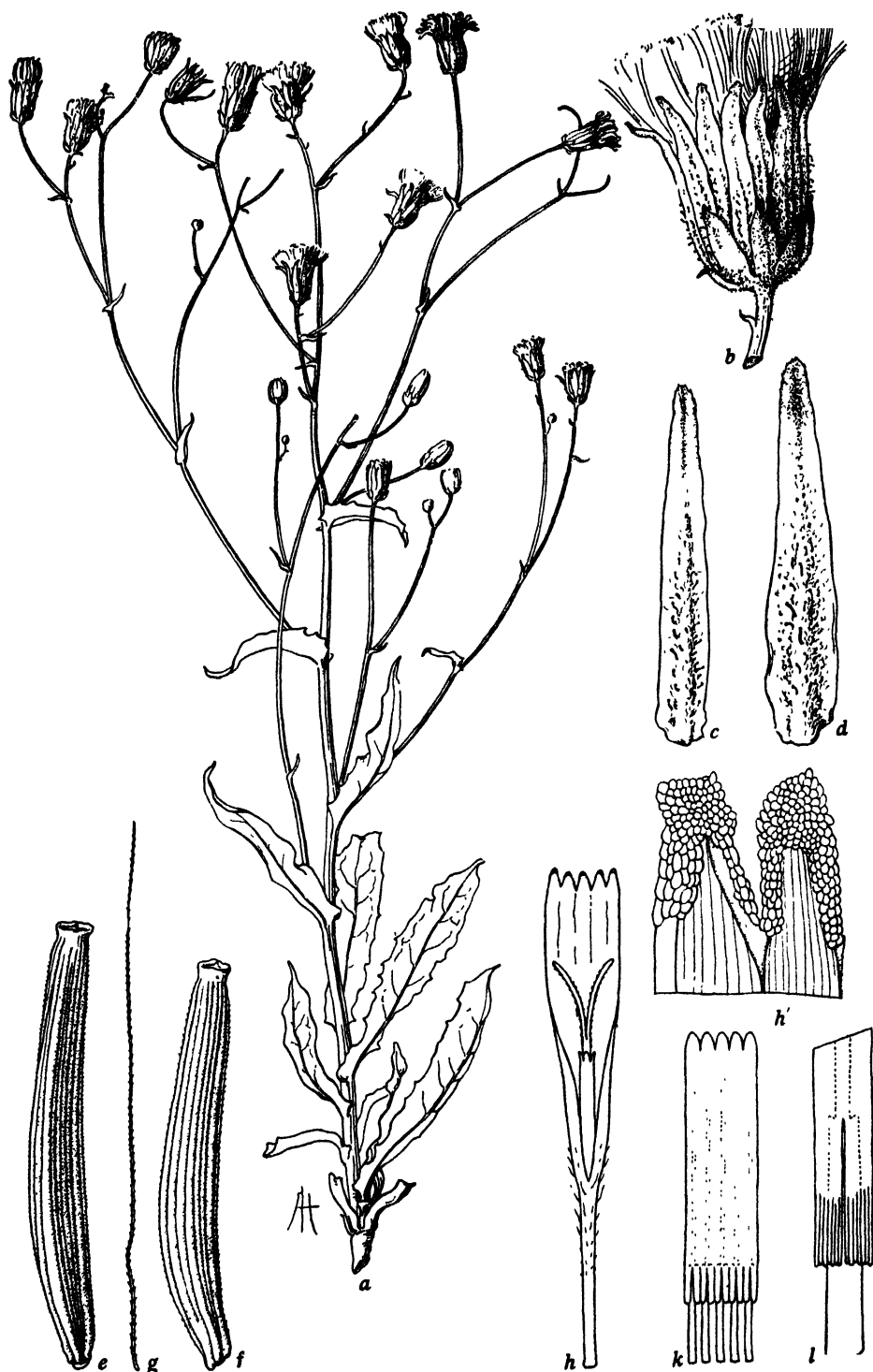


Fig. 102. *Crepis songorica*, from Regel in 1870 (K, UWG): a, plant, $\times \frac{1}{2}$; b, fruiting head, $\times 2$; c, d, 2 inner bracts, outer face, $\times 4$; e-g, 2 achenes and a pappus seta, $\times 8$; h, floret lacking ovary, $\times 4$; h', detail of ligule teeth, $\times 32$; k, anther tube, $\times 8$; l, detail of appendages, $\times 32$.

acute or acuminate, uppermost bractlike; stem simple, erect, terete, striate, \pm gland-pubescent near base, branched above; branches long, spreading, remotely branched; aggregate inflorescence a broad loose compound corymbiform cyme; peduncles 1–6 cm long, arcuate, not thickened near head, with 1–3 linear bracts, glabrous, finely gland-pubescent or tomentose near head; heads rather large, about 30-flowered; involucre campanulate, 12–15 mm high, 5–8 mm wide near base; outer bracts 10, unequal, up to $\frac{1}{2}$ as long as inner bracts, lanceolate, acute, like inner ones pale brownish-green with very dark apices, \pm canescent-tomentose, shortly gland-pubescent, hairs brown; inner bracts 12–14, lanceolate, obtuse, ciliate at apex, membranous on margin, \pm gland-pubescent, becoming dorsally thickened and indurate, glabrous within; receptacle ?; corolla about 17 mm long; ligule about 2.5 mm wide, teeth 0.4–0.6 mm long; corolla tube 6.25 mm long, slender, pubescent with hyaline acicular hairs 0.05–1 mm long; anther tube 4.7×1.25 mm dis.; appendages 0.6 mm long, united, truncate; filaments stout, 1 mm longer; style branches about 3 mm long, 0.2 mm wide, yellow; achenes 8 mm long, reddish-brown with yellow summit, oblong, gradually attenuate upward and moderately constricted below the slightly expanded pappus disk, somewhat narrowed to the broad oblique base, 16-ribbed, ribs unequal in width, rounded, minutely spiculate; pappus white, 8–9 mm long, 3-seriate, the setae unequal, coarsest 50μ wide at base, united at the base, coming away in clumps, persistent, $\frac{1}{3}$ extruded at maturity. Flowering June, July; flowers yellow.

Crepis rigida W. et K. var. *songorica* Kar. et Kir., Bull. Soc. Nat. Mosc., 15: 399. 1842; Ledebour, Fl. Ross. 2: 821. 1844; Regel, Bull. Soc. Nat. Mosc. 40(3): 177. 1867.

Turkestan, Ala-tau Mts., 1200–2300 m alt.

The type locality is described by Karelin and Kirilov (*loc. cit.*) as Ala-tau Mts., between Baskan and Sarchan rivers. This collection of Karelin and Kirilov in 1841 and the following two have not been seen by me: a specimen reported from Kirghis Steppes by Regel (*loc. cit.*); 2 specimens collected by Schrenk in 1840–1843 and reported by Trautvettero (Bull. Soc. Nat. Mosc. 39[2]: 387. 1866), “in promontorio Labaszy, et in promontorio jugi Alatau, ad. fl. Baskan.”

Monomorphic.

Turkestan: Ala-tau Mts., Chanachai R. crossing, 1200 m, *Regel* in 1870 (K, UWG, Mu, NY, UCf); Mt. Chanachai, 1600–2300 m, *Regel* in 1870 (K, UWG, Mu, UCf).

Relationship

Crepis songorica, a little-known species, has long been confused with *C. pannonica*, from which it is easily distinguished by the larger, less attenuate, coarsely ribbed, reddish-brown achenes and longer, coarser pappus; also by the dark-colored involucre, the outer involucral bracts fewer and broader, and the inner bracts gland-pubescent and less tomentose. The leaves in *C. songorica* are also quite different, especially all the cauline leaves sessile with rounded entire base. In habit *C. songorica* produces branches from nearer the base of the plant and the branches are proportionally longer and more remotely branched, thus forming a more open, lax, aggregate inflorescence. *C. songorica* is still further removed from *C. lacera* and *C. chondrilloides*; in fact, it shows more resemblance to *C. darvasica* and *C. Strausii* than to *C. pannonica* and its closest allies.

62. *Crepis sonchifolia* (M. Bieb.) C. A. Mey.

Ex Schrenk, in Fisch. et Mey., Enum. Pl. Nov. 2: 32. 1842. (Fig. 103.)

Perennial, 2.4–6 dm high; caudex straight, slender, elongated, woody, bearing bases of old leaves; caudical leaves lacking; lower cauline leaves up to 15 cm long,

4 cm wide, oblanceolate, lyrate, pinnately divided, terminal segment irregularly dentate, lateral segments remote, triangular or oblanceolate, acute, dentate, rachis narrow, irregularly dentate, attenuate into a short petiole with broader clasping base, chartaceous, hispidulous, spinulose on margin, canescent-tomentulose, veins pale, prominent on lower face; middle cauline leaves similar, sessile; upper cauline leaves much reduced, uppermost bractlike; stem erect, rather stout, branched above or, later, from near base, branches elongated, divaricate, dichotomously 1-2-furcate, not fistulose, tomentulose below, glabrous or sparsely hispidulous above; peduncles of flowering and fruiting heads 6-16 cm long, straight or arcuate, yellow-tuberculate at base, glabrous or obscurely hispidulous, glaucous, 2-3-bracteate, tomentose and \pm sulcate near head; heads erect, rather large, many-flowered; involucre campanulate, about 15 mm high, 6 mm wide near base in fruiting heads; outer bracts 10, unequal, longest $\frac{1}{3}$ - $\frac{1}{2}$ as long as inner bracts, lanceolate or subulate, obtuse at apex, black above, canescent-tomentose at base; inner bracts 12-14, lanceolate, obtuse, white-ciliate at apex, densely canescent-tomentose, with median black line and short black setae, pubescent along margin or near apex on inner face, becoming strongly carinate, thickened at base and indurate in fruit; receptacle areolate-fimbriate, fimbriae 1 mm high, scalelike, deciduous; corolla 20 mm long; ligule 2.5 mm wide; ligule teeth 0.7 mm long; corolla tube 4.5-5 mm long, beset with clusters of coarse stalked acicular hairs up to 0.3 mm long; anther tube about 7×1.5 mm dis.; appendages 0.8 mm long, oblong, obtuse or truncate, strongly united; filaments 1.25 mm longer; style branches 3-3.5 mm long, 0.2 mm wide, attenuate, yellow; achenes dark reddish-brown, 7 mm long, about 1 mm wide, attenuate to the narrow (0.5 mm wide) summit, with abruptly expanded pappus disk, narrowed to the oblique yellow-calloused hollow base, 18-ribbed, ribs nearly equal, extending to pappus disk, close, narrow, rounded, smooth or finely muriculate under lens; pappus white, yellowish at base, 8-9 mm long, 2-3-seriate, rather coarse, stiff but pliable, persistent. Flowering, acc. to Marschall-Bieberstein, July-Aug.; flowers yellow.

Hieracium sonchifolium M. B., Fl. Taur. Cauc. 2: 252. 1808.

E. Caucasus, Daghestan. Radde (370) reports this species as collected by Ruprecht in Daghestan at an elevation between 1818 and 2424 m. Although conceding that this little-known species may not be restricted to Daghestan, the present writer is doubtful about the identity of certain specimens from other regions. This is true especially of the specimens cited under m.v. 1, and two plants from Armenia in herb. Cosson (Paris) which may belong to this species but which require further study to definitely place them.

Daghestan: Achty, *Becker 155* (Lenin), compared with type of M. Bieb., and found to be similar throughout, acc. to N. A. Busch; *ibid.*, *Becker 381* (Bo); *ibid.*, ex herb. Ascherson (B); without locality, *Becker 74* (Bo); *ibid.*, *Becker 259* (Fl, US); *ibid.*, Becker in 1874 (US); † Viasbek, among rocks, *Rehmann 617* (Bo); cult. from seed collected in Daghestan by Becker in 1874 (K ex Herb. Hort. Petropol.).

Minor Variant of C. sonchifolia

1. (*C. sonchifolia* var. *turkestanica* C. Winkl., in herb.) Root and caudex lacking; habit similar to *C. sonchifolia*; leaves similar, not hispidulous; involucre slightly tomentulose, densely pubescent, with long greenish glandless setiform hairs; corolla tube, immature achenes, and pappus similar to *C. sonchifolia*. *Fetisson* in 1881 (B, US), Alexander Mts. (= Alexander-Kette †), Turkestan. [A different collection, without data respecting collector or year, is cited here tentatively, (MW) Sarawschan (Sarafschan †) 1818-2121 m, Turkestan.]

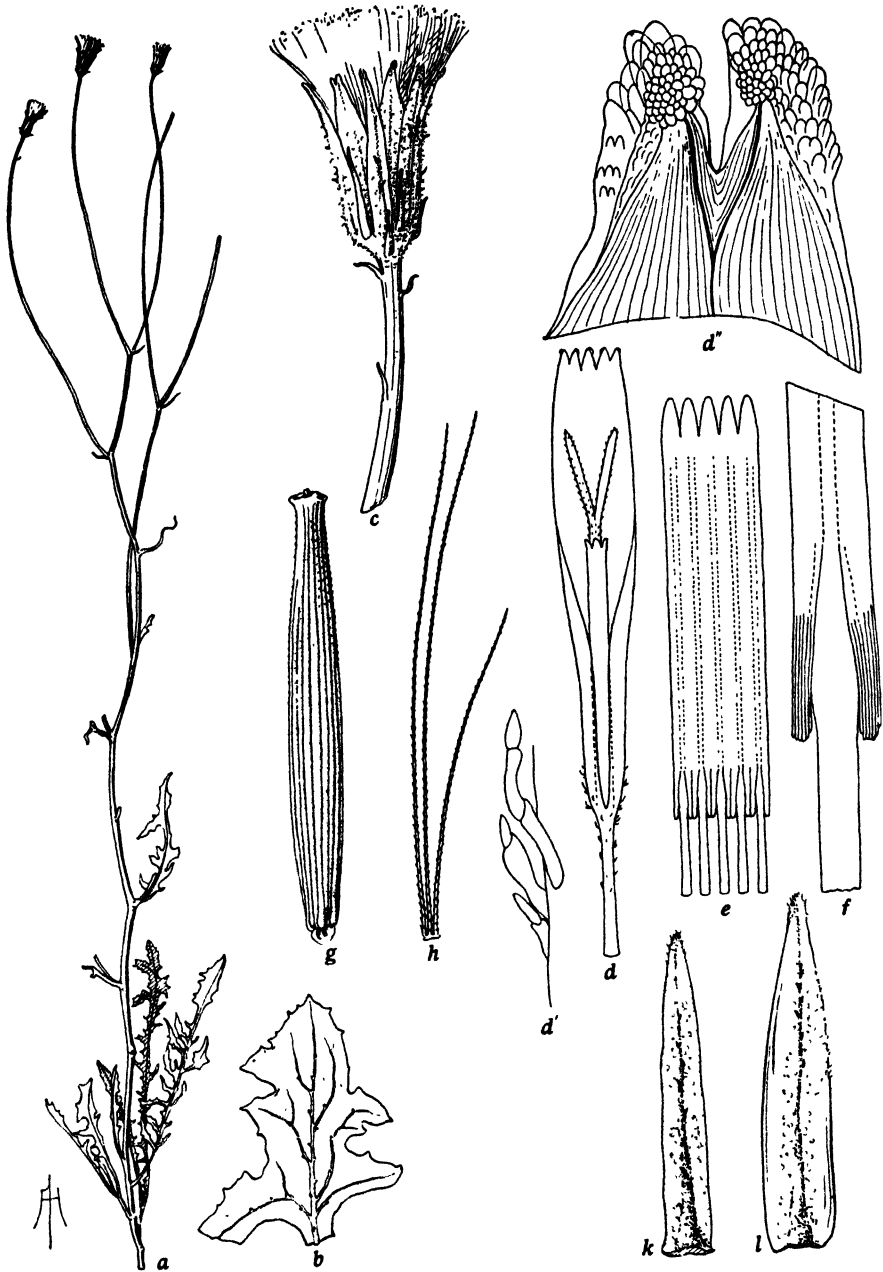


Fig. 103. *Crepis sonchifolia*, from Becker 155 (Lenin, compared with type): *a*, plant, $\times \frac{1}{4}$; *b*, terminal segment of leaf, lower face, $\times 1$; *c*, fruiting head, $\times 2$; *d*, floret lacking ovary, $\times 4$; *d'*, detail of hairs on corolla tube, $\times 50$; *d''*, detail of ligule teeth, $\times 50$; *e*, anther tube, $\times 8$; *f*, detail of appendages, $\times 32$; *g*, *h*, achene and sectional view of pappus setae, $\times 8$; *k*, *l*, 2 inner bracts, outer face, $\times 4$.

Relationship

Crepis sonchifolia resembles *C. songorica*, *C. darvasica*, and *C. Strausii* in its tall corymbiform habit and rather large cauline leaves. Its large florets, anther tubes, and style branches also resemble those of *C. Strausii*. But its pinnatifid leaves, narrower involucre, and more attenuate achenes indicate that it is a somewhat more advanced species than the three preceding ones, suggesting, rather, a connection with *C. macropus* and its allies.

63. *Crepis ciliata* C. Koch.

Linnaea 17: 277. 1843. (Fig. 104.)

Biennial, approximately 6–12 dm high, forming a large rosette the first season and flowering the second; caudical leaves up to 28 cm long, 8 cm wide, oblanceolate or lanceolate, acute, runcinately dentate with narrow acuminate teeth, or pinnatifid with close lanceolate acuminate lateral lobes, the teeth or lobes corneous-mucronate and often retrorse, attenuate into a broadly winged petiole, setulose on both sides with pale glandless setules or only along the prominent midvein and near the margin; lower cauline leaves similar, or lanceolate, sessile; middle and upper cauline leaves lanceolate, acuminate or caudate-acuminate, sessile, amplexicaul, acutely or acuminately auriculate, toward the base dentate or pinnatifid with acuminate mucronate teeth or narrow segments, setulose, especially along the margin; stem erect, robust, about 1 cm wide at base, strongly sulcate, densely to sparsely setose with pale glandless setae, cymosely branched above, the branches strict, elongated, 1–6-headed, forming a compound corymbiform aggregate inflorescence; peduncles 1–20 cm long, strict or arcuate, setulose, tomentulose, somewhat enlarged near the head, sometimes with 1 or 2 bracts near the head, rarely bearing 1 or 2 small leaves; heads erect in all stages, medium to large, about 70-flowered; involucre campanulate, 12–13 mm high, 8–12 mm wide in fruit, canescent-tomentulose, densely setose with yellowish usually long glandless setae; outer bracts 7–9, unequal, longest about $\frac{2}{3}$ as long as the inner, lance-linear, obtuse, white-ciliate at apex, green below, blackish toward apex, becoming lax and incurved at the margin; inner bracts 11–13, lanceolate, obtuse or acute, white-ciliate at apex, scarious-margined, densely pubescent on inner face with appressed white hairs, becoming carinate dorsally, medianly concave ventrally, and only slightly spongy-thickened at the base at full maturity; receptacle alveolate, fimbriellae membranous, finely ciliate, the cilia white, from extremely short to 1–2 mm long; corolla about 16 mm long; ligule about 2.5 mm wide, pubescent on lower $\frac{1}{3}$ of outer face with acicular hairs up to 0.3 mm long; teeth about 0.5 mm long; corolla tube 4–5 mm long, pubescent with papilliform trichomes 0.05–0.1 mm long; anther tube (4)5 × 1.5 mm dis.; appendages 0.6 mm long, oblong, obtuse; filaments 1 mm longer; style branches about 3 mm long, 0.1 mm wide, yellow; achenes pale brown or tawny, 4.5–6 mm long, 0.8–1 mm wide, fusiform, slightly more attenuate upward, 0.3–0.5 mm wide at the scarcely expanded pappus disk, abruptly constricted at the very narrow pale-calloused hollow base, 18–20-ribbed, ribs nearly equal, sometimes 3–5 slightly stronger, narrow, rounded, smooth or muriculate under lens; pappus white, 6.5–8 mm long, 2-seriate, the setae unequal in length, about equally fine in width, the coarsest about 30 μ (5 cells) wide, rather soft, united into a ring at the base, coming away in small clumps, persistent. Flowering, under cultivation in California, in midsummer; flowers yellow. Chromosomes, $2n = 40$, 42 ?

Hieraciodes ciliatum O. Kuntze, Gen. 1: 345. 1891.

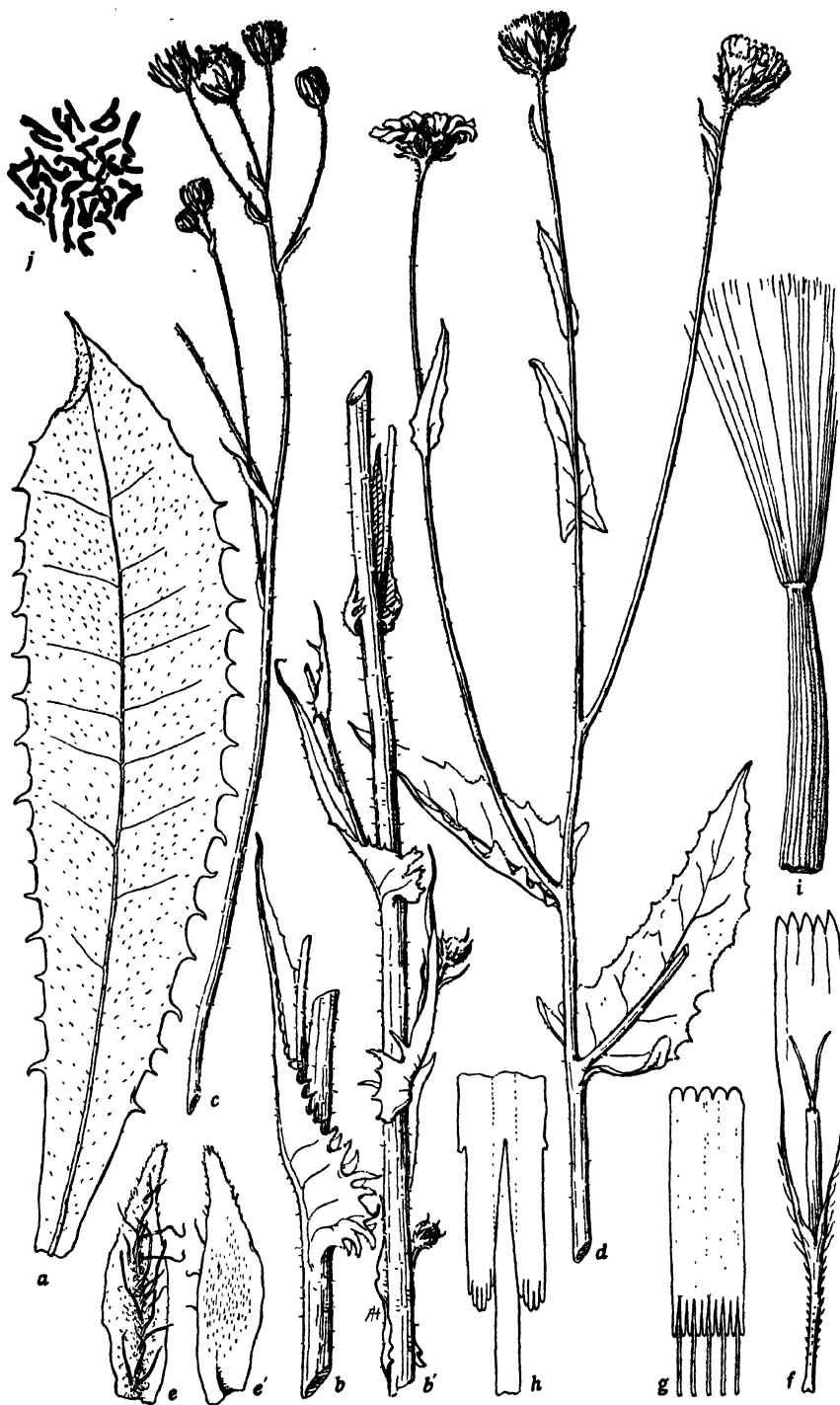


Fig. 104. *Crepis ciliata*, a-c, e-h, from type (B); d, from a plant collected by Fischer (Lenin); i, from a plant collected by Sch. Bip. (PC); j, from hort. genet. Calif. 2181 (grown from seeds received from the Caucasus through Dr. M. Navashin): a, caudical or lower cauline leaf, $\times \frac{1}{2}$; b, b', parts of stem, $\times \frac{1}{2}$; c, terminal part of aggregate inflorescence, $\times \frac{1}{2}$; d, upper part of a nearly mature plant, $\times \frac{1}{2}$; e, e', inner involucre bract, outer and inner faces, $\times 4$; f, floret lacking ovary, $\times 4$; g, anther tube, $\times 8$; h, detail of appendages, $\times 32$; i, part of an immature achene with pappus, $\times 8$; j, somatic chromosomes, $2n = \text{about } 40$ ($x = 5$), $\times 1250$.

Transcaucasia, in Georgia and Armenia.

Monomorphic, as far as known.

The only definite locality known to the present author is Achalkalaki (Akal-kalaki), which appeared on a packet containing seed of this species received from Dr. M. Navashin of Moscow. (Unfortunately no herbarium specimens were made from this accession [2185], but chromosome counts of 3 plants were reported as 40, 42 ♀ 42 ♀.) Since there are 2 towns of this name in Georgia, the exact source of the seed is uncertain. One town is northwest of Tiflis on a tributary of the Kura R. at an altitude of approximately 600 to 900 m; the other is southwest of Tiflis on the Toporovan R. at an altitude of approximately 900 to 1800 m. Since the latter is closer to N. Armenia, it is perhaps the more likely locality. At any rate, this species, like *C. biennis*, is apparently a plant of lower elevations.

Another locality (also dubious) is given on the label of a specimen collected by Koch which is deposited in herb. Cosson (Paris). This name is apparently Daradschitschak. Daradschi, in Aderbeidschan (Azerbaijan), N.W. Persia, is only about 400 km southeast of N. Armenia and 600 km from S. Georgia; and it is situated at an elevation between 600 and 900 m. Possibly the name in question is a modification of Daradschi, resembling the name Turknantschai, a neighboring city of Aderbeidschan.

Transcaucasia: Armenia, *ex herb. Koch* (B, UCf) type; "southern Caucasus," *ex hort. genet. Calif.* 30.2181, cult. from seed obtained through M. Navashin, seed packet bears the name "Kabriaz" (UC). **Persia** (♀): Aderbeidschan (♀), Daradschitschak (= Daradschi ♀), *Koch*, *ex herb. Sch. Bip.* (PC, UCf). **Without Locality:** *ex herb. Fischer* (Lenin).

Relationship

Crepis ciliata strongly resembles the preceding members of this section in the tall corymbiform habit, the numerous large cauline leaves, the rather large heads, the fairly primitive type of involucre, and the many-ribbed achenes. From what has been seen of its somatic chromosomes, it appears to be an octoploid, with the basic chromosome number, $x = 5$; but evidence is lacking regarding the meiotic behavior of its chromosomes. Although it is an extremely vigorous plant and occurs at lower elevations, it has never become a widespread weed of European fields, as is true of *C. biennis*. This may be due to the isolation of *C. ciliata* at a few localities in the broken mountainous reg. south of the crest of the Caucasus, whereas *C. biennis*, developing north of the crest, was able to migrate, perhaps with man's unconscious aid, into the lowlands to the northwest. The fact that *C. biennis* is certainly and *C. ciliata* probably an octoploid may indicate a remote origin, an origin which is supported by the present wide distribution of *C. biennis*. Certainly the two species have sufficient morphological and cytological resemblance to warrant the assumption of their common ancestry.

Although the simplest hypothesis would be that the two species originated through isolation of two or more forms of a common octoploid ancestor, a comparison of the chromosomes of the two species does not seem to support such a simple assumption (cf. B. and Sw.). It is more probable that they evolved from closely related diploid ancestors which became isolated as a result of the elevation of the Caucasus during the Miocene. This is in agreement with the concept that the numerous endemics in this and related sections of *Crepis* represent the isolated offshoots of ancestral species which were widespread in the Iran-Caucasus-Asia Minor-Balkan land area in mid-Tertiary time.

64. *Crepis biennis* L., Sp. Pl. 2: 807. 1753.

(Pl. 7. Fig. 105.)

Biennial, 2–12 dm high, from a woody elongated or much branched root, forming a rosette the first year, not flowering usually until the second; caudex and base of stem 0.2–1.3 cm wide; caudical leaves 5–25 cm long, 1.5–7.5 cm wide, oblanceolate, acute, denticulate, dentate, runcinate-pinnatifid, or pinnately parted, with triangular terminal lobes and remote lanceolate entire or dentate lateral lobes, the teeth or lobes corneous-mucronate, attenuate into a narrowly winged petiole, scabridulous on both sides with fine yellow glandless setules; lower cauline leaves similar, middle and upper lanceolate to linear, sessile, acute, acuminate or caudate-acuminate, pinnatifid to entire, uppermost bractlike; stem erect, slender to very robust, striate to sulcate, \pm setulose or glabrescent, cymosely or paniculately branched above the middle or from near the base, branches elongated, strict, few-branched above, 1–6-headed, making a simple or compound corymbiform aggregate inflorescence; peduncles 0.5–1.6 cm long, strict or arcuate, striate or sulcate, \pm thickened near the head, glabrescent, canescent-tomentulose, or \pm setulose with yellow or black glandless setules; heads erect, medium to large, 30–100-flowered; involucre campanulate in fruit, 8–13 mm high, 5–9 mm wide at middle, pale or dark green or nearly black, \pm canescent-tomentose, sometimes silky-pubescent and often setulose with yellow or black setules on inner bracts; outer bracts 7–9, nearly equal, $\frac{1}{2}$ – $\frac{2}{3}$ as long as the inner ones, lance-linear, acute, glabrous or tomentulose, becoming lax and scarious; inner bracts 10–17, lanceolate, acute, white-ciliate at apex, scarious-margined, appressed-pubescent on inner face, becoming dorsally carinate, medianly concave on inner face, and only slightly spongy-thickened near the base at full maturity; receptacle alveolate, fimbriae low, sparsely and very shortly ciliate; corolla 12–18 mm long; ligule 2–2.3 mm wide, pubescent on lower $\frac{1}{3}$ of outer face; teeth 0.25 mm long; corolla tube 3–5.5 mm long, pubescent with 2–3-celled acicular trichomes 0.1–0.3 mm long; anther tube (3.75) 5.5 \times 1.25 (1.5) mm dis.; appendages 0.75–1 mm long, oblong, obtuse or acute; filaments 0.5–0.6 mm longer; style branches 2.25–3.5 mm long, 0.15 mm wide, yellow or rarely green; achenes stramineous, yellowish or pale brown, rarely cinnamon brown (cf. m.v. 2), 4–7.5 mm long, 0.6–1 mm wide, equally attenuate to both ends or more gradually attenuate upward, with slightly expanded pappus disk about $\frac{1}{2}$ as wide as the achene, constricted at the pale-calloused hollow base, 10–20 (usually 13–18)-ribbed, ribs nearly equal, narrow, rounded, muriculate or spiculate near the apex under lens; pappus white, 5–7 mm long, 2–3-seriate, the setae unequal in length, about equally fine, coarsest setae 50–65 μ wide at base, rather soft, united into a ring at the base, coming away in small clumps, persistent. Flowering June–Aug.; flowers yellow. Chromosomes, $2n = 40 \pm$.

Crepis scanensis L., It. Scan. 170. 1751, *fide* DC., Prod. 7: 163. 1838.

Hedypnois biennis Huds., Angl. 342. 1762, *fide* DC., *loc. cit.*

C. muricata Gilib., Ft. Lithuan. 3: 231. 1781, *fide* Ledeb., Fl. Ros. 2: 823. 1844–1846.

C. lodomeriensis Bess., Prim. Fl. Gall. 2: 150. 1809 et DC., Prod. 7: 163. 1838 excl. syn.

C. Gmelini Schultes, Fl. Oestr. 2: 419. 1814, non Tausch.

Barkhausia pinguis Rehb., Fl. Exc. 1: 257. 1830–1832 excl. syn.

C. maritima Boucher, Fl. d'Abbeville, ed. 3, 59. 1834, *fide* Rouy, Fl. Fr. 9: 229. 1905.

C. glandulosa Bast., ex Moesal., Handb. ed. 3, 2: 1475. 1833, non Guss.

C. sabauda Balb., ex DC., *loc. cit.*

Hieracium dienne Karach, Fl. Westf. 330. 1856.

C. lacera Fiori, Fl. Anal. Ital. 3(2): 436. 1904, non Tenore.

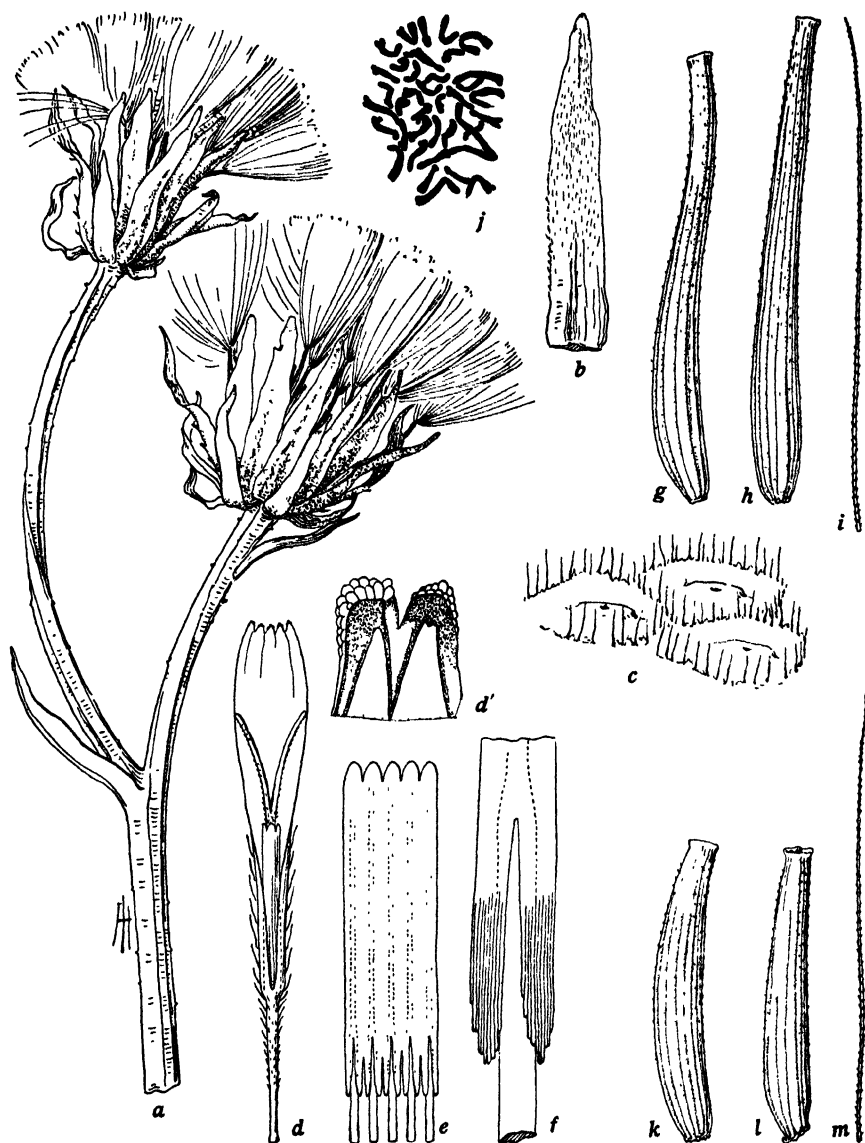


Fig. 105. *Crepis biennis*, a-i, from Hall 12559 (UC 346486); j, from hort. genet. Calif. 27.1874, plants grown from seeds received from Bot. Gard. Univ. Cluj; k-m, from Hall 12561 (UC 326487): a, branchlet with 2 heads, $\times 2$; b, inner bract, ventral face, $\times 4$; c, detail of receptacle, $\times 25$; d, floret lacking ovary, $\times 4$; d', detail of ligule teeth, $\times 25$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g-i, 2 achenes and a pappus seta, $\times 8$; j, somatic chromosomes, $2n = \text{about } 40$ ($x = 5$), $\times 1250$; k-m, 2 achenes and a pappus seta, $\times 8$.

Middle Europe, from middle Spain, France, and N. Italy to the British Isles and S. Norway and Sweden; eastward through the Baltic states to central Russia (Kazan); and from Italy, Switzerland, and the Low Countries through Germany, Austria, Rumania, the Balkan Pen. south to Macedonia, S. and middle Russia. It has also been reported from the N. Ural Mts., from Samarkand, Russian Turkestan, and from Brusa, Anatolia, in all of which regions it may be adventive. It has been introduced into North America (cf. Long, B., *Rhodora* 21: 209-214. 1919) and

probably into other parts of the world as a result of its frequent occurrence in meadows and fields and its consequent distribution with seeds of forage plants (cf. Hegi, 1164–1165). Although it is characteristically a lowland species, it has been reported to occur in mountainous regions at elevations from 900 to 2000 m.

In view of its wide distribution and considerable altitudinal range, it is perhaps not surprising to find extreme variability in size of the plant, and of the stem, leaves, heads, flowers, and fruits. But the most frequent variations have been in the occurrence and degree of dissection of the leaves, and many floras have recognized three named varieties based mostly on these small differences (cf. Bischoff, 268): (a) *runcinata* Koch; (b) *lacera* Wimm. et Grab.; (c) *dentata* Koch. Individual authors have added still other names to this list of "leaf-shape varieties." Although such variations in leaf outline have been proved to have a true genetic basis in *Crepis capillaris*, it has also been shown that their degree of expression is very susceptible to environmental changes. Hence, it seems hardly worth while to recognize these leaf variations here even as numbered variants. Of greater significance is the fact that a number of extreme morphological variants have been reported, a few of which have been recognized as varieties or even species. Some of these are undoubtedly teratological in nature, such as, for example, var. *prolifera* DC. (*loc. cit.*) and the virescent form shown by Hegi (fig. 842). In addition, several other minor forms are discussed by Hegi (*loc. cit.*). It is not known, however, whether any of these forms represent geographic races or subspecies. Accordingly, several, not including those mentioned by Hegi, will be cited below and described as numbered variants. Certain of these variants may be of theoretical interest to the cytogeneticist. Further consideration of polymorphism in *C. biennis* is given in the concluding paragraphs.

Because of this polymorphism, *C. biennis* is often confused with other species, especially by those who are satisfied with superficial resemblance. *C. nicaeënsis*, because of the general similarity in habit and leaves, is the species most often misidentified as *C. biennis*. But, in addition to the almost unfailing difference of presence or absence of hairs on the inner face of the inner involucre bracts, the outer bracts of the involucre are longer and wider in *C. biennis*, and the achenes are longer, different in shape, and usually have more than 10 ribs. Because determinations were made from inadequate herbarium specimens, *Crepis oporinoides* became confused at one time with *C. biennis*, and at another time with *C. nicaeënsis*. The corrected identities of these three species, including a synoptical comparison, have been published (Babcock, Jour. Bot. 73:224–227, 1935). De Candolle's *C. biennis* β *americana* was based (with reservation) on Hooker's misidentification of specimens of *C. runcinata* as *C. biennis*. The two species are very unlike.

Denmark: "Scania," Linne 11 (L) type. **Sweden:** Landskrona, Tullberg (Bur); Gotland, Fole, St. Tollby, Fries in 1931 (UC); Skåne, Fetterstedt in 1873 (Minn). **England:** E. Yorkshire, Burton Agnes, Lawson in 1929 (Oxford); N. Somerset, between Cheddar and Axbridge, White in 1906 (Bur); Surrey, Kew, Trail (Minn). **Belgium:** Anchie, near Dinant, along Meuse R., Moosenos in 1933 (UC). **France:** Lyon, Mt. Verdun, 550 m, Hall 12559, 12560, 12561 (UC); Gers, Masseube, Prés, Duffort 931 (UC); Haute Savoie, Pringy, Luget in 1868 (US); Savoy, near Cessens and Chatelard, Pin in 1883 (K); Isère, Fontaine, Pellat in 1886 (Grenoble); without locality or collector (DC. Herb. Prod. VII. 163 n. 15), 1 sheet, as *C. sabauda* Balb., 2 sheets, var. *prolifera* DC. teratological, 1 sheet, *ex herb. Roche*, typical except achenes cinnamon brown; Seine infer., Treport, Brutelette in 1860 (Bur); *ibid.*, cliffs of Treport. *Soubeyran* in 1881 (DL), as *C. maritima* Boucher = m.v. 1. **Italy:** Aprutii, near Isola, 700–800' m, Rigo in 1906 (Bur). **Switzerland:** Bex, valley of the Rhone, Hall 12610 (UC); near Genève, Ayasse in 1884 (Bur, Minn); Buchanbez, Braun-Blanquet 397 (Ms); Berne, near Lenk, 1100–1200 m, Burnat in 1917 (Bur); Vallais, Thiers Valley, Burnat in 1853 (Bur). **Germany:** Palatinate, near Deidesheim, Schultz Bipontinus in 1844 (Bur); without locality, hort. bot. Berol. (B), as *C. lodomeriensis*;

Halle, near Wittekind (Minn); Bavaria, Würzburg, *Gross* in 1906 (UC); near Dresden, *Wolf* in 1894 (UC); near Valbenburg, *Tap* in 1917 (UC); E. Prussia (†), Spanden (†), *Conrad* in 1895 (Minn). Austria: near Mauer, *Halassy* (Bur, Minn); near Aistersheim, *Keck* (Bur, Minn); Tirol, Trini Eggarten, *Kerner* in 1892 (UWG). Rumania: Transylvania, Hagy Enyed (†), *Csato* in 1891 (Minn). Bulgaria: Mt. Pirin, 1250 m, *Georgieff* in 1932 (UC); Mt. Vitoscha, *L.T.* in 1932 (UC); Roslog dist. (E. Macedonia), Bansko, moist meadow, *Georgieff* in 1932 (UC) typical, except style branches green; *ibid.*, Bansko, moist meadow, *Georgieff* in 1932 (UC) m.v. 2. Russia: Ukraine, Shitomir Prov., *Golde* in 1890 (UC); Kaluga Prov., near Kaluga, *Litvinov* in 1894 (Bur); Leningrad reg., fields and margins of woods, higher elevations, in 1866 (UC).

Minor Variants of *C. biennis*

1. (*C. maritima* Boucher, *loc. cit.*) Low and bushy habit, branching mostly from the base, the branches or peduncles elongated; leaves thick, dentate or entire; involucre slightly pubescent, the bracts all obtuse. "Very rare." Probably the result of some sort of chromosomal variation. *Soubeiran* in 1881 (DL), base of cliffs, Treport, Seine infer., W. France.

2. Very slender, plants 2.7–4 dm high, few-headed, with nearly entire leaves only 1 cm or less in width, but the stem and branches typical in habit; heads small, 30–40-flowered; involucre 7–9 mm high, 4–6 mm wide in fruit; flowers and flower parts at the lower limit of size for the species, otherwise typical; achenes cinnamon brown, 4.5 mm long; pappus typical. Chromosomes, $2n = 40$. Such brown achenes are very unusual but have been seen in one otherwise typical specimen in herb. DC. Since typical plants were collected at or near the same station by *Georgieff*, it is a question whether such low, slender plants are not caused by crowding or some other repressive factor. But the dark-colored achenes are probably due to a genetic factor or factors. *Georgieff* in 1932 (UC), moist meadow, Bansko, Roslog dist. (E. Macedonia), Bulgaria.

3. (*C. biennis* e *maxima calva* Schur, Verh. Naturf. Verein Brünn 36: 209–211. 1897.) Plants up to 13 dm high, with wide-spreading branches, dark green, glossy; stems, leaves, and involucre almost glabrous, glossy; leaves very unequally divided, sagittate-auriculate at the base. Spec. not seen by me, but description suggests that these plants may have had double the normal number of chromosomes, i.e., about 80 instead of 40. A few such plants have occurred among our garden cultures. Acc. to Schur, Sept., 1867, bed of the Alserbach (River †), Dornbach and Weinhaus, near Vienna.

4. (*C. biennis* f *sonchiformis* Schur, *loc. cit.*) Plant 10 dm high, slender, erect, remotely leaved; stem terete, fistulose; leaves runcinate, pale bluish-green, somewhat gray; aggregate inflorescence falsely umbelliferous; branches very long, erect, glabrous; peduncles simple or furcate, woolly near the head and sparsely black-setose. The cause of such an abnormal form, pending further information, can only be a matter of conjecture, but chromosomal variation might be involved. Spec. not seen. Acc. to Schur, July–Aug., oat fields, with *Sonchus arvensis*, in Siebenbürgen near Kronstadt and in Mähren on the yellow hills near Brünn.

5. (*C. biennis* h *humilis crassicolis* Schur, *loc. cit.*) Root elongated, branched, with one or several flower stems; caudex thick, globose; stems 3 dm high, mostly branched from base or simple, at summit falsely umbelliferous to 3-headed; heads small, up to 13 mm long, rounded at base; peduncles and involucre white-woolly, green, bracts smooth and brown at apex; basal leaves runcinate, upper ones linear, dentate or entire; flowers gold-orange colored. Another abnormal form, the cause of which is unknown; but Schur's description suggests that the environment may have been largely responsible. Spec. not seen. Acc. to Schur, in stony, sunny places, on dams, near Neustift, Brünn.

Relationship and Variability

Crepis biennis, like *C. ciliata*, shows strong general resemblance to the other species in this section. *C. biennis* is an octoploid with the basic chromosome number, $x = 5$; and probably *C. ciliata* is also an octoploid. But it does not seem likely that the two species were derived from a common octoploid ancestor. It is more probable that they evolved from closely related diploid ancestors which became isolated during the elevation of the Caucasus Mts. From evidence concerning chromosome morphology it has been inferred (cf. B. and Sw.) that *C. biennis* may have originated as an amphidiploid which later doubled its diploid chromosome sets, whereas *C. ciliata* is more probably an autopolyploid species. It is possible also that this may account for the widespread distribution of *C. biennis*. It certainly is consistent with the high polymorphism of this species.

The commonly occurring variations in *C. biennis*, such as size of parts, shape of

leaves, and color of achenes, fall in the general category of gene mutations. The phenotypic expression of such mutations would more likely occur in an amphioctoploid than in an autoöctoploid species, assuming of course that, in the former, pairing of chromosomes at meiosis takes place, as a general rule, between like members of the same tetraploid set. It has been shown (cf. C., H., and A.) that, in a hybrid between *C. biennis* and *C. setosa*, the 20 *biennis* chromosomes form 10 pairs at first meiotic metaphase. In an $8x$ autopolyploid, multivalents would be expected to occur and the distribution of any one of the eight chromosomes of a given type would be at random with respect to its combinations with the other seven. Hence, a simple gene mutation which had occurred in some one of the eight chromosomes would have a much smaller chance of ultimate phenotypic expression through recombination in the progeny of an autoöctoploid than in an amphioctoploid. But occasional chromosomal aberrations would be expected to occur in either type of polyploid; and some of the abnormal forms which have been reported are very probably due to such causes. In this connection the following observations are of interest.

Among the progeny of the hybrid between *C. biennis* and *C. setosa* mentioned above, Collins obtained a plant possessing 10 pairs of *biennis* and 2 pairs of *setosa* chromosomes. Its first generation of progeny was fairly uniform both in morphology and in chromosome number, and the new race was named *C. artificialis*. In succeeding generations, however, numerous variants have appeared, some with different chromosome numbers. The chromosome numbers which have thus far been found among the later progenies, derived from the original 12-paired *C. artificialis* plant by repeated selection, range from 20 to 36. This certainly indicates a considerable amount of irregularity in meiotic behavior, caused, probably, by a tendency of the *C. biennis* chromosomes to form polyvalents. But this does not invalidate the hypothesis that *C. biennis* originated as an amphidiploid, since artificially produced amphidiploids between *Crepis rubra* and *C. foetida* were found by Poole (Univ. Calif. Publ. Agr. Sci. 6: 231–255. 1932) to have a large amount of meiotic irregularity due to polyvalent formation.

Crepis biennis is less closely related to the following species than to *C. ciliata* and the more primitive members of this section. At the same time it exhibits sufficient resemblance to *C. nicaeënsis* to mark it as a connecting species between sec. 24 and the more primitive species of this section. It is clear, however, that cytogenetic evidence supports the placing of *C. biennis* in sec. 10 rather than in sec. 24. In the first place, the most primitive species in sec. 10 that have been examined cytologically have $n=5$ chromosomes, and the base number of *C. biennis* is $x=5$; whereas *C. nicaeënsis*, the most primitive species in sec. 24, has $n=4$. Of greater significance is the fact that, in F_1 hybrids between *C. setosa* and these other two species, there was no pairing between the chromosomes of *C. setosa* and those of *C. biennis* (see Part I, p. 16), in contrast with regular pairing with those of *C. nicaeënsis* (see Part I, p. 56). Thus, the genome of *C. nicaeënsis* must be much more similar to that of *C. setosa* than is the basic genome of *C. biennis*.

65. *Crepis pannonica* (Jacq.) K. Koch

Linnaea 23(7): 689. 1851. (Figs. 106, 107.)

Perennial, 3–13 dm high; root vertical, stout, woody; caudex 0.3–1 cm wide in single-stemmed plants, in very robust specimens larger and bearing several stems; caudical leaves 15–30 cm long, 4–6 cm wide, oblanceolate to elliptic, acute, dentate, corneous at apex of teeth and sometimes along margin, attenuate into a long (or short) winged petiole, rather thick, firm, scabrous, densely or sparsely setulose with

pale glandless setules, \pm gland-pubescent; lowest cauline leaves similar, sometimes with petioles longer and narrowly winged or shorter and more broadly winged than the caudical leaves, the others obovate, elliptic, ovate or lanceolate, acute or acuminate, dentate, sessile, amplexicaul, roundly or acutely auriculate, gradually reduced, but in robust plants still conspicuous, even at the lower branches of the inflorescence, uppermost bractlike, in reduced plants the leaves all relatively narrower; stem erect, woody, and 0.3–1 cm wide at base, terete, sulcate, setulose, and sometimes glandular below, tomentulose or glabrescent above, leafy throughout, the leaves close, overlapping, or sometimes remote, branched above middle or near summit, the branches short, all about equal, and 1–8-headed, thus forming a simple raceme, or cymosely compound or paniculate, or all or the uppermost branches elongated, corymbiform, the branches strict or arcuate, rigid, sulcate; peduncles 0.2–5 cm long, stout, rigid, sulcate, tomentulose or glabrescent, often with 1–3 bracts near the head; heads erect, medium to large, 50–90-flowered; involucre cylindric-campanulate, 10–15 mm long, 6–9 mm wide at middle in fruit, pale to rather dark green, \pm tomentulose to canescent-tomentose; outer bracts 10–12, unequal, longest $\frac{1}{2}$ as long as inner ones, lance-linear, acute, darker and white-ciliate at apex, becoming lax; inner bracts 12–15, lanceolate, acute, darker at the white-ciliate apex, sometimes with a few short glandless setae, glabrous on inner face, becoming strongly carinate dorsally and concave ventrally, strongly indurate, yellowish-brown and slightly spongy-thickened near the base; receptacle alveolate, fimbriate white-ciliate; corolla 15–18 mm long; ligule 2.5–2.75 mm wide; teeth 0.25–0.4 mm long; corolla tube about 5 mm long, sparsely pubescent with stout acicular hairs up to 0.6 mm long; anther tube about 5×1.5 mm dis.; appendages 0.6–0.75 mm long, oblong, truncate; filaments 0.5 mm longer; style branches 2.75–3 mm long, 0.15–0.18 mm wide, yellow; achenes brown, pale near apex, 5–6 mm long, 0.9–1.1 mm wide, subterete, fusiform, attenuate to the narrow apex (0.3–0.4 mm wide), with expanded white-edged pappus disk, constricted at the small oblique pale-calloused hollow base, 15–20-ribbed, ribs nearly equal, relatively narrow but somewhat variable in different plants, rounded, muriculate under lens; pappus white, 5–8 mm long, 3-seriate, the setae about equally fine, coarsest about 30μ (4 cells) wide, rather soft, deciduous. Flowering June–Aug.; flowers yellow. Chromosomes, $2n = 8$.

Hieracium pannonicum Jacq., Coll. 5: 148. 1796.

Crepis rigida Waldst. et Kit., Pl. Rar. Hung. 1: 18, t. 19. 1802.

C. latifolia Balb., ex Pers., Syn. Pl. 2: 377. 1807.

Brachyderea rigida Cass., Dict. 48: 430. 1827.

Crepis Blawii Asch., Zeits. Ges. Erdkunde, Berlin, 1870: 549.

Mulgedium Blawii Asch., Bot. Ztg. 1879: 260.

Hieraciodes pannonicum O. Kuntze, Gen. 1: 345. 1891.

Hungary, Lower Austria, Istria, and Yugoslavia; locally in Bohemia, Moravia, Bulgaria (Dobrudja), Rumania (Siebenbürgen steppes), Poland (and Lithuania ?); central and S. Russia, including Crimea; Caucasus, Transcaucasia, and N.W. Persia; N.W. Kazakstan, acc. to Pavlov (367), on the high steppes of Turgai north of the Aral Sea; Ural Mts., acc. to Karelin et Kirilov (Bull. Soc. Nat. Mosc. 15: 399. 1842) and Ledebour (821).

In central Europe, acc. to Hegi (1140), it grows on sunny hills, shrubby slopes and grassy borders, and in pastures and fields. Koch (*loc. cit.*) states that on the plain of Ossa (Poland ?) it occurs on tertiary and diluvial soil, and in Gaue Daikh (Gaudyke, Lithuania ?) on secondary lime and marl. In Krasnodar Prov., Russia, along the foot of the mountains southeast of Novorossiisk, acc. to Radde (159, 162),

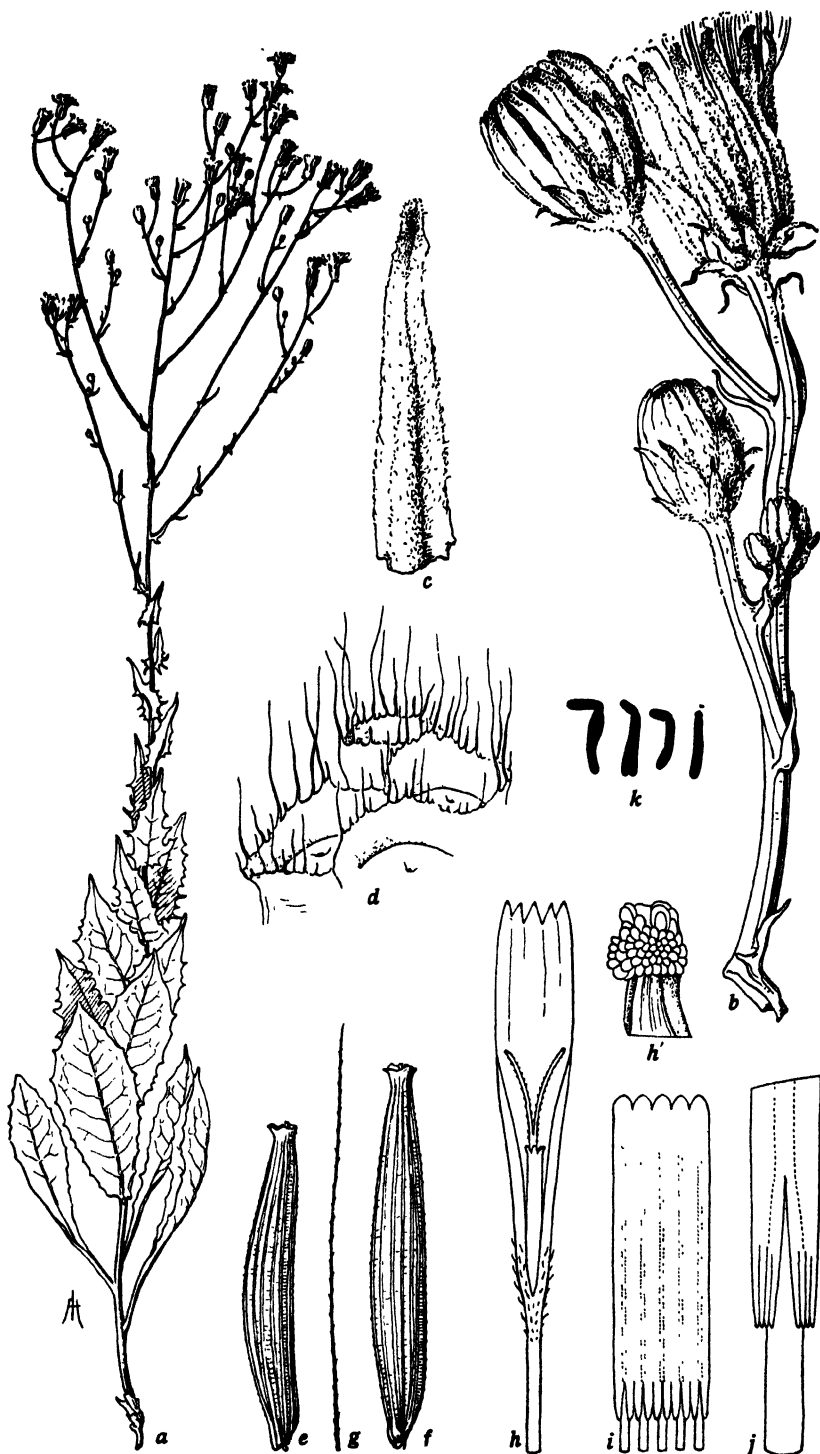


Fig. 106. *Crepis pannonica*, a plant with corymbiform inflorescence, from hort. genet. Calif. 28.1695-8 (UC 633235): *a*, plant, $\times \frac{1}{6}$; *b*, 3 heads, $\times 2$; *c*, inner involucre bract from a mature head, outer face, $\times 4$; *d*, detail of receptacle, $\times 25$; *e-g*, 2 achenes and a pappus seta, $\times 8$; *h*, floret lacking ovary, $\times 4$; *h'*, detail of ligule teeth, $\times 32$; *i*, anther tube, $\times 8$; *j*, detail of appendages, $\times 32$; *k*, somatic chromosomes, $n = 4$, $\times 1250$.

a distinct plant association is characterized by rough-hairy herbs which are often pyramidal in habit. Here this species (listed as *C. rigida*) is associated with species of *Verbascum*, *Echium*, *Phlomis*, etc. On the N.E. slope of the Caucasus Mts., from Chassaf-jurt to the S. slope of the high range (Radde, 249), the soil is calcareous and the annual rainfall is 50–100 cm. The "Paliurus-Maqnis" flora flourishes in this area. Along with *Scabiosa ochroleuca*, growing more than a meter high, robust specimens of *C. pannonica* (*C. rigida*) were collected. Certainly this species is a plant of lower elevations, although its exact altitudinal limits are unknown. I have seen specimens collected at 200 m and at 1400 m.

The types of Jacquin and of Waldstein and Kitaibel have not been seen by me, but the two descriptions are essentially similar, and the synonymy of *C. rigida* W. et K. has been generally recognized. In herb. DC. (Prod. vii: 160–162) I saw 5 sheets of *C. rigida* W. et K., 1 of which was from Schrader (Hort. Gött.) in 1811; and in herb. Burnat, a specimen of *C. rigida* W. et K. from the type locality of *C. rigida*.

The only variations of importance in this species are concerned with the habit of the aggregate inflorescence. Jacquin describes it as paniculate, and the excellent illustration of Waldstein and Kitaibel (*loc. cit.*) agrees with that description. In 14 herbarium specimens now before me, all have a paniculate or racemose inflorescence; but in 3 or 4 of them the topmost 4 or 5 branches in themselves make a corymbiform cluster like that shown in Reichenbach (Ic. Fl. Germ. et Helv. 19: t. 96. 1858–1859). Furthermore, in garden cultures grown from seed collected in Budapest by Dr. Javorka, my plants have a corymbiform aggregate inflorescence, the lower branches being much elongated. But Karelin and Kirilov (*loc. cit.*) describe 2 varieties of *C. rigida* W. et K., var. *communis* of middle Russia and var. *Lessingiana* of the Ural Mts. From the descriptions the second differs from the first only in being more scabrous and in having the involucre gland-pubescent. Both forms are described as having the branches of the inflorescence *abbreviated*, which variability in the habit of the inflorescence is referred to again under m.v. 1. Two other varieties which have been recognized on the basis of glandulosity are var. *adenophylla* Rohlena (Vierter Beit. Fl. Montenegro, Sitz. Ges. Wiss. Vestnik 38: 66. 1904) and var. *viscosissima* Rohlena (*loc. cit.*). The habit of the inflorescence, however, is not described, and both habit forms occur in the W. Balkan Pen.

Hungary: Budapest, open grassy slopes above O-Buda, type locality of *C. rigida* W. et K., Simonkai (Bur, Minn); *ibid.*, Mt. Faborberg, Degen in 1920 (UC); Kutgavár, among shrubs, Tauscher in 1871 (Bur); near Offen-Pest and Altöfen, Freyn in 1872 (UWH); Bude Dolomit, Richters in 1876 (DS). **Austria:** Mt. Bisamberg, near Wien, Vestergrén in 1922 (UWG). **Istria:** Carstiana, Mt. Lipnik, Justin in 1910 (UWG) m.v. 1. **Bosnia:** Livno-Linj, about 1000 m, Stadlmann et al., in 1904 (UWG, UWH) m.v. 1; Tusnica dist., 1200–1300 m, Stadlmann et al., in 1907 (UWG, UWH) m.v. 1. **Dalmatia:** near Otosic, south of Vrlika, Janchen et Watsel in 1907 (UWG). **Montenegro:** Piva dist., Bortovici, about 1400 m, Rohlena in 1905 (Mu) as var. *adenophylla*. **Transcaucasia:** Georgia, Caucasus, mountain pastures, Hohenacker in 1834 (CA, Mo); Armenia, Alaghez dist., near Kosha-Bulog, 2100 m, Busch in 1930 (G). **Persia:** Elburz Mts., near Asadbar (Asadber), Kotschy 454 in 1843 (Mo), the notation, "m. Elbrus," is obviously a misspelling.

Minor Variant of C. pannonica

1. (*C. Blawii* Asch., *loc. cit.*; *Mulgedium Blawii* Asch., *loc. cit.*; *Crepis rigida* Vis., Fl. Dalm. 2: 119. 1847.) (Fig. 107.) Aggregate inflorescence strictly racemose or paniculate, not at all corymbiform, and the leaves and lower stem densely gland-pubescent. Although maintained as a species by Stadlmann (Oester. Bot. Zeits. 58: 422–425. 1908), the only points of difference between it and *C. pannonica* which are mentioned by him are those stated above. As has already been shown, this species, with respect to habit of the inflorescence, is variable throughout its range. The fact that the two types of inflorescence, corymbiform and paniculate, are faithfully maintained in adjoining garden cultures shows that they have a genetic basis. But there

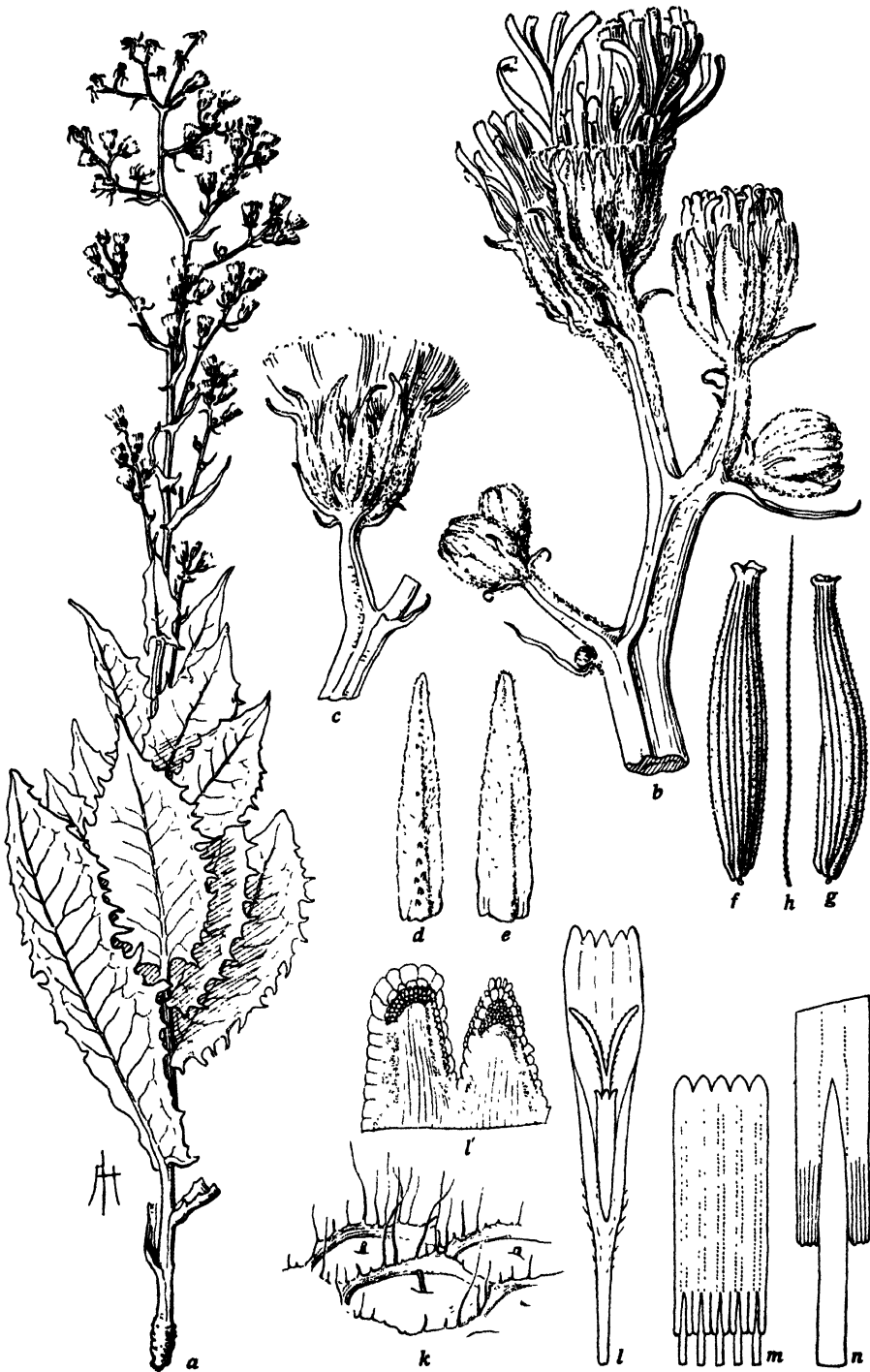


Fig. 107. *Crepis pannonica*, m.v. 1, a plant typical of *C. Blawii* Asch., hort. genet. Calif. 27.1672-2 (UC 633228): *a*, plant, $\times \frac{1}{4}$; *b*, flowering heads and buds, $\times 2$; *c*, fruiting head, $\times 2$; *d, e*, 2 inner involucre bracts, outer face, $\times 4$; *f-h*, 2 achenes and a pappus seta, $\times 8$; *k*, detail of receptacle, $\times 25$; *l*, floret lacking ovary, $\times 4$; *j*, detail of ligule teeth, $\times 32$; *m*, anther tube, $\times 8$; *n*, detail of appendages, $\times 32$.

is plenty of evidence to indicate that any population of the species may be capable of producing either type. At any rate, the racemose type occurs in Hungary, Persia, and the Ural Mts. Moreover, Jacquin's description mentions the paniculate habit, and the authentic illustration of *C. rigida* W. et K. portrays it. As would be expected, plants of this form intercross freely with plants of corymbiform habit in the garden, and the hybrids are very fertile. Variations in degree of glandulosity also occur generally throughout the range of the species. In addition to the following cited specimens, it has been reported from Dalmatia, Hercegovina, and Montenegro. *Justin* in 1910 (UWG), Mt. Lipnik, Carstiana, Istria; *Stadlmann et al.* in 1904 and 1907 (UWG, UWH, UCf), Livno-Linj and Tusnica, Bosnia.

Relationship

Crepis pannonica is the only widespread diploid species in this section. This wide distribution, together with its fairly primitive involucre, indicate that it is nearly as old as the four preceding species, even though they are somewhat more primitive in their flowers and achenes. Among the other species in the section, *C. lacera* and *C. chondrilloides* are closest to *C. pannonica*, although *C. bertiscea* and *C. ciliata* also exhibit much resemblance, whereas *C. biennis* is less close.

66. *Crepis latialis* Sebast.

Rom. Pl. 2: 16, t. 5. 1815. (Fig. 108.)

Perennial, 2–6 dm high; root vertical, woody, crowned with the short brown-scaly slightly thicker caudex; caudical leaves up to 20 cm long, 8 cm wide, oblanceolate, obovate or elliptic, acute, runcinate-pinnatifid to pinnately parted or bipinnatifid, terminal lobe rhombic or triangular to linear-acuminate, lateral lobes lanceolate to linear, entire, denticulate, dentate, or pinnately lobed, gradually reduced toward apex and base, petiole about $\frac{1}{2}$ as long as the blade, narrowly winged, broader, scarious and spongy-thickened at the base, sometimes with short brown wool at the very base, lightly tomentulose or sparsely setulose, ciliate at margin, the teeth and lobes corneous-mucronate; lowest cauline leaves similar, the others sessile, pinnatifid and caudate-acuminate, or linear, entire, uppermost bractlike; stem erect, straight or sinuate, robust, rigid, sulcate, tomentose at base and bifurcations or throughout, sometimes pale-setose and glandular, sometimes glabrescent, paniculately branched from about the middle or higher, making a compound racemiform to subcorymbiform inflorescence, or also remotely branched from near base, the lower branches elongated, strict, racemosely branched near summit; peduncles 0.5–6 cm long, divaricate or arcuate, rigid, often bracteate, glabrescent or tomentulose, slightly thickened near the head; heads erect, medium, 40–50-flowered; involucre cylindric-campanulate, 8–11 mm high, 5–7 mm wide at middle in fruit, canescent-tomentose, sometimes with short black glandless setae; outer bracts 7–10, unequal, longest $\frac{1}{3}$ – $\frac{2}{3}$ as long as the inner, linear, acute; inner bracts 12–16, lanceolate, acute or obtuse, glabrous or sparsely strigose near tip on inner face with appressed shining trichomes, becoming dorsally carinate, pale spongy-thickened and somewhat indurate, ultimately reflexed; receptacle areolate-fimbriate, fimbriae thin, naked; corolla about 13 mm long; ligule 2 mm wide, shortly pubescent on lower half of outer face; teeth about 0.5 mm long; corolla tube about 4 mm long, pubescent with papilliform or short acicular hairs; anther tube about 4×1.2 mm dis.; appendages about 0.7 mm long, lanceolate, acute; filaments about 0.6 mm longer; style branches 2 mm long; achenes dark reddish or purplish-brown, 4.5–6 mm long, 0.9–1.3 mm wide, fusiform, more strongly attenuate toward apex, sometimes with a neck or very short coarse beak about 0.3 mm wide, with slightly expanded white pappus disk, constricted at the pale-calloused hollow base, 16–20 (mostly 18)-ribbed, ribs unequal, with a tendency to be alternately stronger and weaker, rounded, smooth,

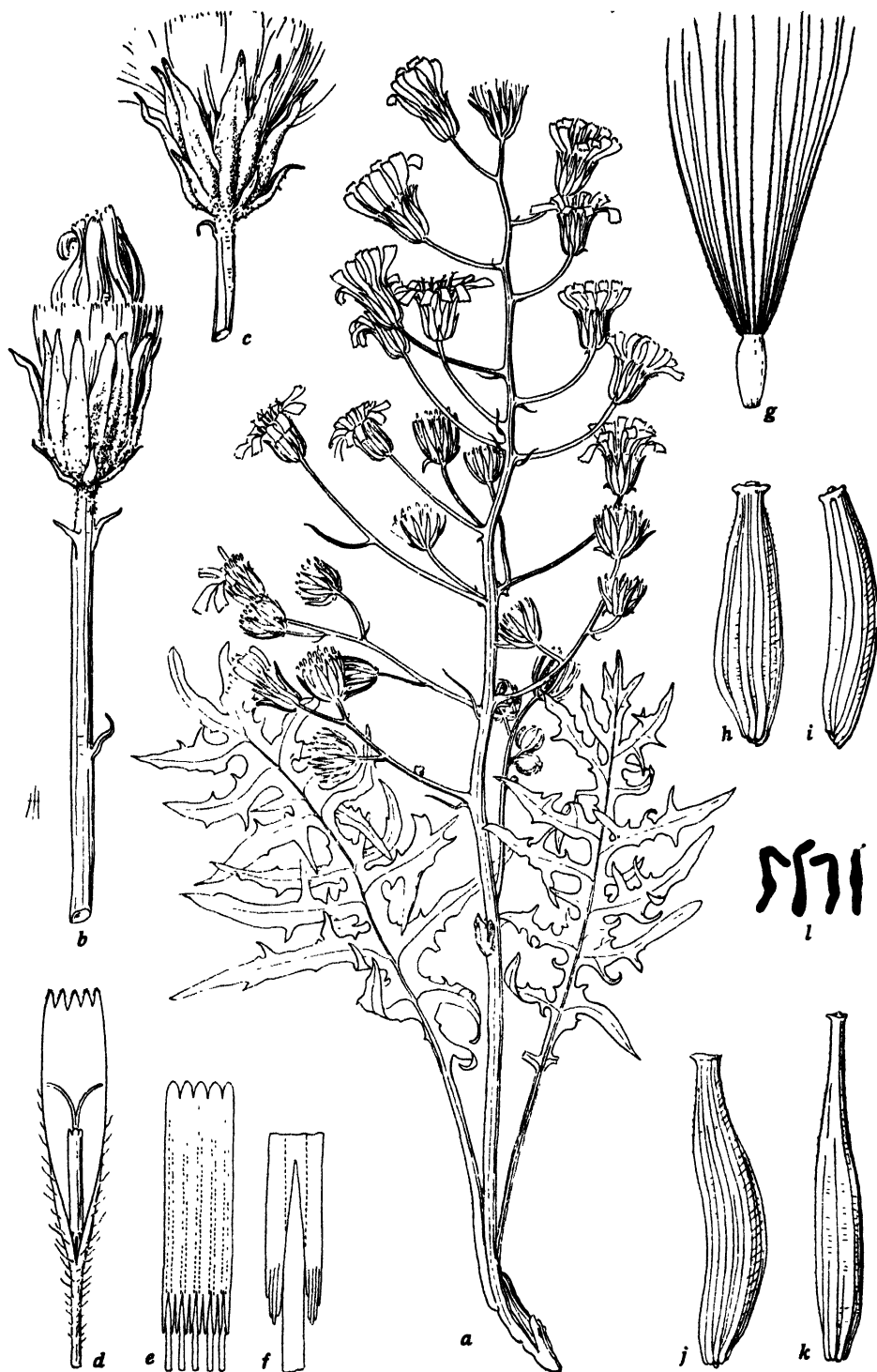


Fig. 108. *Crepis latialis*, *a*, from an authentic spec. of *C. lacera* Ten. in herb. Tenore (from a photograph); *b-g*, from Gussone in 1824 ex Herb. Neapol. (UC 259892); *h-k*, from seeds received from the Naples Bot. Gard.; *l*, from hort. genet. Calif. 1914 (grown from seeds received from Naples Bot. Gard.): *a*, plant $\times \frac{1}{2}$; *b*, flowering head, $\times 2$; *c*, mature head, $\times 2$; *d*, floret lacking ovary, $\times 4$; *e*, anther tube, $\times 8$; *f*, detail of appendages, $\times 32$; *g*, immature achene with pappus, $\times 8$; *h-k*, achenes, $\times 8$; *l*, somatic chromosomes, $n = 4$, $\times 1250$.

or muriculate under lens; pappus white, 5.5–6.5 mm long, 3-seriate, setae nearly equally fine, the coarsest about 40μ (5 cells) wide, soft, persistent. Flowering June–July; flowers yellow. Chromosomes, $2n = 8$.

Crepis biennis Seb. et Maur., Fl. Rom. Prod. 272. 1818, non L.

C. lacera Tenore, Fl. Neapol. 2: 179, t. 74. 1820.

C. erucaefolia Tausch, Flora 11 (I Erg.): 34. 1820, non Gr. et Godr.

Hieraciodes latiale (Sebast.) O. Kuntze, Gen. 1: 345. 1891.

Italy, from about 44° N. lat. to the southern end of the peninsula; submontane and montane, from near sea level to 1400 m alt.; on calcareous soil; endemic.

The type has not been seen by me, but the original description and illustration are sufficient to identify the species.

Although very variable in its leaves, particularly in size, number of lobes, size and shape of the lobes, and, as indicated above, somewhat variable in the character of the aggregate inflorescence, yet only one subspecific entity has been named. This is f. *titani* Pamp., based on the wholly runcinate caudical leaves and unusually wide upper leaves of this plant, which was collected in the Republic of San Marino, presumably on Mt. Titano, one of the farthest north localities thus far reported. The only other more northern station known to me is Bologna (cf. Fiori, 437). It may be inferred that this species is fairly constant throughout its range, except for local modifications due to environmental factors. It is reported (de Candolle, 161) to be an extremely poisonous plant (*fide* Tenore et Gussone) and to have medicinal value for heart ailments.

Italy: Rome, Mt. Lucretile, *Sanguinetti* (Rome), as *C. lacera* Ten., *C. latialis* Sebast.; Campania, Napoli, *Tenore* in 1814, *Sebastiani* in 1817, *Gussone* in 1831 (DC); Campania, Avellino, Montevergine, *Pellanda* in 1911 (US, G, UC); Calabria, Cosenza, Mt. Dirupata di Morano, *Rigo* 352 (Bur, US); *ibid.*, *Huter* 424 (US, Mo); Apulia, Gargano, Mt. S. Angelo, *Porta et Rigo* in 1874 (Mo, UC); Apulia, 1–727 m, *Porta et Rigo* in 1874–1875 (Ms); Abruzzi, Pettorano, *Gussone* in 1826 (Naples, UC); Abruzzi, near Caramanico, *Pellanda* in 1911 (US); Abruzzi, above Rocca-val-oscuro, *Ilult* 376 (Bur); Abruzzi, between Paganica and Assergi, near Aquila, *Leresche* in 1876 (Bur); Abruzzi, Villa Vallelonga, *Grande* in 1826 (UC); Abruzzi, Majella Mts., *Pedicino* in 1872 (P); Republica di San Marino, *Pampanini* (Fl) as *C. lacera* f. *titani* Pamp.

Relationship

Crepis latialis is intermediate between *C. pannonica* and *C. chondrilloides*, and artificial hybrids between *C. latialis* and both the other two species are 5–10 per cent seed-fertile in the open. But *C. latialis* is isolated geographically from the others. Although very similar morphologically, the three species are easily distinguished by their leaves, and they differ in many other details. Of the other members of this section, *C. bertiscea* is next in order of relationship to this species.

67. *Crepis bertiscea* Jáv.

Magyar Bot. Lap. 21: 21. (1922); Csiki, Javorka et Kümmerle, Additamenta ad Floram Albaniae, Budapest, t. xxi. 1926. (Fig. 109.)

Perennial, 5–6 dm high; root long, vertical, woody, 1 cm wide below the leafy caudex; (caudical leaves [*fide* Jávorka] oblong, acute, lyrate-runcinate, sinuately dentate, the teeth elongated gradually, narrowly oblong or linear, acuminate, sometimes unequally acutely dentate); lower cauline leaves 15–19 cm long, 3–6 cm wide, the blade elliptic, acute, sublyrately pinnatifid, the terminal part incompletely segmented and acuminately dentate, lateral segments numerous, close, lance-linear, acuminate, denticulate or entire, growing shorter toward apex and base of blade, gradually attenuate into a winged petiole, glabrous above, tomentulose on lower face along midvein; middle cauline leaves linear, acuminate, entire, sessile, am-



Fig. 109. *Crepis bertiscea*, from type (Budapest): *a*, whole plant, $\times \frac{1}{4}$; *b*, part of old head and peduncle, $\times 2$; *b'*, inner face of same, $\times 2$; *c*, inner involucre bract, inner face showing groove which enclosed achene, $\times 4$; *d*, achene, and *e*, pappus seta, $\times 8$.

plexicaul, acutely auriculate; uppermost leaves bractlike; stems 2, erect, robust, puberulent below, glabrescent above, paniculately 5-branched from about the middle, branches strict or arcuate, 1–3-headed, the aggregate inflorescence about 10-headed; peduncles 1.5–7 cm long, striate, constricted just below the head and sometimes pale spongy-thickened confluent with receptacle; heads erect, medium,

about 100-flowered; involucre campanulate, 10–12 mm high, 7–9 mm wide at middle in fruit, canescent-tomentulose; outer bracts about 6, about $\frac{1}{3}$ as long as the inner, appressed, lance-linear, acute; inner bracts about 12, lanceolate, acute, glabrous on inner face, becoming dorsally carinate and prominently pale spongy-thickened confluent with the receptacle and summit of peduncle; receptacle areolate, glabrous; florets (*fide* Jávorka) yellow; achenes dark brown, 5.5–7.5 mm long, 0.8 mm wide, oblong or fusiform, strongly attenuate upward into a neck or coarse beak about 1.5 mm long and 0.3 mm wide, with slightly expanded white pappus disk, constricted at the lightly calloused small hollow base, 13–18-ribbed, ribs nearly equal, rather prominent, narrow, rounded, extending to pappus disk, muriculate under lens; pappus white, about 5.5 mm long, probably multiseriate, deciduous. Flowering Aug.–Sept.; flowers yellow.

Known only from the type collection of 2 plants, one merely a rosette without flower stem. The specific name was derived from “Bertiscus,” a name used by Strabo for the reg. where this plant was collected.

Monomorphic.

Albania (†): N. Albanian Alps, Mt. Skelsen (= Skülßen †), steep, E. slope, above the small stream Tropoja, in calcareous gravel, 1200 m, with *Lunaria Telekiana* and *Micromeria rupestri*, Jávorka in Sept., 1918 (Budapest, photograph and fragments in UC).

Relationship

Crepis bertiscea is close to *C. latialis*, as was noted by Jávorka, who also classified it under *Berinia* (Brign.). But, as Jávorka points out, *C. bertiscea* differs from *C. latialis* in leaf shape, the thicker, fistulose peduncles, and the usually longer, coarsely beaked achenes. Although the achenes of *C. latialis* are sometimes nearly as long and as definitely beaked as those of *C. bertiscea*, yet those of *C. latialis* are broader and have more ribs. Also the involucre of *C. latialis* are sometimes setose, and they become less prominently spongy-thickened at maturity. *C. latialis* has never been reported from the Balkan Pen. *C. bertiscea* is less close to *C. chondrilloides*.

68. *Crepis chondrilloides* Jacq.

Enum. Vindob. App. 312. 1762, non *Hieracium chondrilloides* L., nec Jacq. (Fig. 110.)

Perennial, 2–5.5 dm high; root vertical, woody, few-branched, elongated, 3–8 mm wide at summit, merging into the leafy caudex; caudical leaves numerous, forming a dense rosette, withering later, 6–16 cm long, 1.5–5 cm wide, oblanceolate, acute, pinnately divided to the midvein into very numerous close linear or filamentous entire or 1-toothed segments, glabrous or puberulent, petiole $\frac{1}{3}$ – $\frac{1}{2}$ as long as the blade, not alate; lower cauline leaves similar or sessile, the others often reduced to the narrow rachis, or small and bractlike; stem erect, terete, striate or sulcate, canescent-tomentulose or tomentose, often setose with yellow setae bearing brown glands, branched near summit, forming a short few-headed simple or compound raceme, or branched from below the middle, the lower branches elongated, making a subcorymbiform paniculate inflorescence; peduncles 1–13 cm long, stout, arcuate, sometimes constricted near the head, canescent-tomentose, often setose, with or without glands; heads erect, medium, 50–75-flowered; involucre campanulate, 11–14 mm long, 6–8 mm wide at middle, canescent-tomentose, the inner bracts often setulose, with yellow or sometimes black setules, with or without glands; outer bracts 8–10, very variable in size, the longest $\frac{1}{4}$ – $\frac{1}{2}$ or $\frac{2}{3}$ as long as the inner, linear or lanceolate, acuminate, becoming scarious and lax; inner bracts 12–16, lanceolate, acute, white-ciliate at apex, glabrous or sparsely appressed pubescent toward apex

on inner face, becoming yellowish-carinate dorsally and toward the base swollen and spongy-thickened confluent with the receptacle at full maturity; receptacle alveolate, fimbriellae low, densely ciliate, cilia white, 3 mm long; corolla about 15 mm long; ligule about 2 mm wide; teeth 0.75–3 (mostly about 1.5) mm long; corolla tube

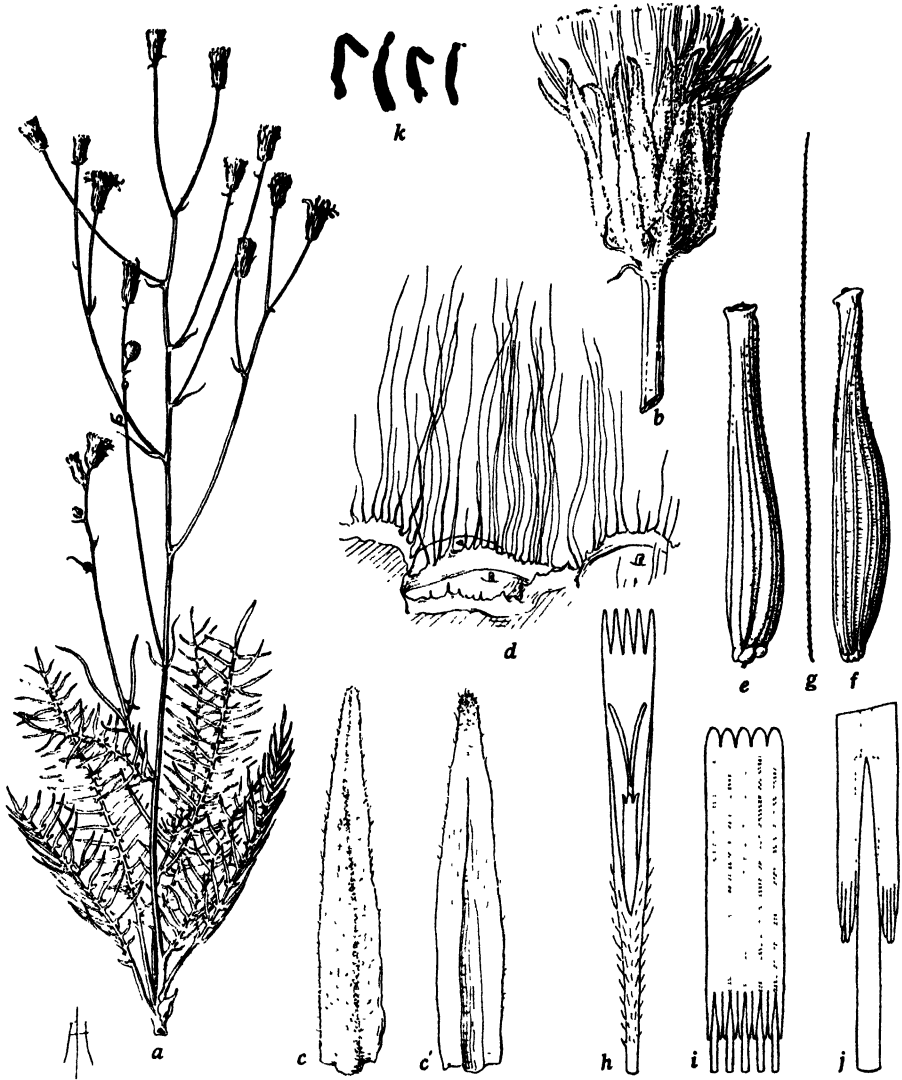


Fig. 110. *Crepis chondrilloides*, a–j, from hort. genet. Calif. 28.2180–3 (UC 639598); k, from hort. genet. Calif., 1907 (grown from seeds collected at type locality through Dr. A. Fiori, Firenze): a, plant, $\times \frac{1}{4}$; b, fruiting head, $\times 2$; c, c', inner involucre bract, outer and inner faces, $\times 4$; d, detail of receptacle, $\times 25$; e–g, 2 achenes and a pappus seta, $\times 8$; h, floret lacking ovary, $\times 4$; i, anther tube, $\times 8$; j, detail of appendages, $\times 32$; k, somatic chromosomes, $n = 4$, $\times 1250$.

about 5 mm long, densely pubescent with stout several-celled trichomes; anther tube about 5×1.3 mm dis.; appendages about 0.75 mm long, lanceolate, acute; filaments 0.5 mm longer; style branches 3 mm long, 0.15 mm wide, yellow; achenes brown or dark brown, 5–7 mm long, 0.7–0.9 mm wide, fusiform, more strongly attenuate upward, sometimes with a very coarse short beak, with slightly expanded pale pappus disk, somewhat constricted at the rather broad pale-calloused hollow

base, 14–18-ribbed, ribs rather strong, rounded, muriculate under lens; pappus white, 7–8.5 mm long, 3–4-seriate, the setae unequal, outermost shorter and finer, the coarsest up to 50μ (5 cells) wide at base, stiff but pliable, persistent. Flowering May–June; flowers yellow. Chromosomes, $2n = 8$.

Andryala chondrilloides Scop., Fl. Carn. 2: 115, t. 52. 1772.

Berinia andryaloides Brign., Forojul. 50. 1810.

Crepis adonis Spreng., Pl. Min. Cog. Pugill. 1: 54. 1813.

Wibelia chondrilloides Hoppe et Hornsch., Tageb. 278. 1818.

C. foeniculacea Rehb., ex Moessl., Handb. ed. 2, 1: 1401. 1828; Froel., ex DC., Prod. 7: 172. 1838.

Hieracium foeniculaceum Wulf., ex Moessl., loc. cit. as syn.

Brachyderca chondrilloides Sch. Bip., ex Nym., Consp. 456. 1878–1882.

Hieracioides andryaloides O. Kuntze, Gen. 1: 345. 1891.

C. andryaloides A. Kerner-Fritsch, Sched. 9: 70. 1902, non Lowe.

N.E. Italy and W. Yugoslavia; Istria, in the Karst reg. south of a line connecting Zoll and Adelsberg (*fide* Hegi, 1162), also littoral; from Illyric Krain (Carniola) to Bosnia, Dalmatia, Hercegovina, and Montenegro. Forming colonies in fields and on grassy, stony places, this, acc. to Hegi (*loc. cit.*), is one of the best known species of the open country in the Karst reg. It occurs from nearly sea level up to 800 m elevation.

Although the type has not been seen by me, Jacquin's description is full and accurate and the illustration of Reichenbach (Ic. Fl. Ger. Helv. 19: t. 95. 1858–1859) is excellent. Excepting minor variations in size of the plant and its parts, this species appears to be very constant. There have been reports of 2 forms with entire leaves. Scopoli (*op. cit.*, 116) mentions one form in which the caudical leaves were entire, the result, he believed, of excessive nutriment. Tommasini (Flora 20: 474. 1837) reports a form in which the plants on each side of the entire-leaved form had the usual laciniate leaves. If the remarkable dissection of the leaves in this species were due to a single gene mutation, it would not be surprising to find an occasional entire-leaved plant. In this connection it is of interest to note that the earliest juvenile leaves of this plant are entire and that with increasing age they become progressively denticulate, dentate, pinnately lobed, and at length laciniate.

Monomorphic.

Istria: Karst, mts. above Trieste, Pichler in 1870 (K, US); *ibid.*, Mt. Spaccato, calcareous soil, 200–400 m., Marchesetti 1395, 3408 (Bur, Genoa, K, Po, Minn); *ibid.*, Fiori et Bégunot 1395 (K); *ibid.*, Schultz Bipontinus 58 (K), as *Brachyderca chondrilloides*; *ibid.*, Tommasini 1438, 1495 (Ms, K); N. Istria, Mt. Lipnik, 800 m, Justin in 1910 (UWG). **Croatia:** near Fiume, Smith in 1891 (UC); Lika-Krbava, Sensjko Bilo Mts., Mt. Pisarola, Senj (Zengg), Dobiasch in 1913, 1916 (US, UC). **Bosnia:** Tusnica dist., S. slope of the Vitrnjak, Stadlmann et al. in 1907 (UWG); Bosnia (?), between Profecto and Obzina, ex herb. Wulfen (UWM), as *Hieracium foeniculaceum*.

Relationship

Crepis chondrilloides is closely related to *C. latialis* and *C. pannonica*. First generation hybrids between *C. chondrilloides* and *C. latialis* were 5–10 per cent fertile, as estimated from the number of open-pollinated seed produced. But these two species never come in contact with each other in nature. First generation hybrids between *C. chondrilloides* and *C. pannonica* were wholly or nearly sterile. Stadlmann (Oesterr. Bot. Zeits. 1908[11]:4) has reported a natural hybrid between *C. chondrilloides* and the form of *C. pannonica* commonly known as *C. Blawii* (cf. \times *C. Malyi*). He states that the pollen of the hybrid was largely fertile; but even if this were so, it would not necessarily follow that the plant would set much seed. It would hardly be expected to be fertile, since our artificial hybrids between the two species were sterile. At any rate, *C. chondrilloides* comes in contact with *C. pannonica* only to a very limited extent.

69. ***Crepis bupleurifolia*** (Boiss. et Kotschy) Freyn et Sint.

Ex Freyn, Oest. Bot. Zeitsch. 42: 268. 1892. (Figs. 111, 112.)

Perennial, 3–6.5 dm high; root . . . ; caudex \pm brown-woolly; caudical leaves few, glabrous, glaucescent, up to 12 cm long, 4 cm wide, oblanceolate, acute, lyrate pinnately parted, terminal segment oblong or ovate, hastate, lateral segments few, remote, ovate to lanceolate, gradually diminishing downward, petiole 3–5 cm long, with broader clasping base; lower cauline leaves similar or longer, shortly petioled or sessile, narrowly auriculate, middle ones lanceolate, acute or acuminate, cordate-amplexicaul, dentate or entire, uppermost abruptly reduced, linear, bractlike; stem erect, sinuate, terete, striate, pale green, glabrous, fistulose, paniculately branched above middle or from near base, branches shorter than axis, rather strictly erect, paniculate-corymbiform, few-headed, like peduncles yellow-tuberculate at base; peduncles 0.5–2 cm long, rather stout, not changed in fruit, like branches and involucre densely pubescent with fine short brown gland hairs; heads erect, medium, about 12-flowered; involucre obconical, base narrow, 3–5 mm wide at middle, up to 13 mm high; outer bracts 7–8, unequal, longest $\frac{1}{4}$ – $\frac{1}{2}$ as long as inner bracts, lanceolate, acute or acuminate, appressed; inner bracts 8–10, lanceolate, acute, ciliate at apex, glabrous on inner face, becoming dorsally carinate, pale spongy-thickened at base; corolla in marginal florets 16 mm long; ligule widest near summit; teeth unequal, acuminate; corolla tube pubescent with very short coarse hairs; anther tube slightly narrowed near base; style branches 2.25 mm long, yellow; achenes pale yellowish-brown, 5.5–6.5 mm long, fusiform, gradually narrowed to the strongly calloused base, moderately to strongly attenuate to the slightly expanded pappus disk, subterete, 5-costate, costae broad, separated by narrow grooves, each costa striate or definitely 3-ribbed; pappus white, 4.5–6.5 mm long, 2–3-seriate, setae nearly equally fine, coarsest about 30μ wide at base, rather brittle, deciduous. Flowering July–Aug.; flowers yellow.

E. Asia Minor in W. Kurdistan and W. Armenia, high montane.

Only 3 collections are known to the author. These have been published as two different species, the type of the species having been dubiously classified, in the absence of mature fruits, as *Sonchus* by Boissier. Although this plant was transferred to *Crepis* in 1892, the author of the second species does not refer to it, yet the two are certainly one specific entity. The only question involved is one of subspecific rank. The scanty material available exhibits numerous though minor differences. For the present, therefore, the two will be treated as subspecies.

Key to the Subspecies of Crepis bupleurifolia

- Outer involucreal bracts $\frac{1}{3}$ – $\frac{1}{2}$ as long as inner bracts; achenes 6.5 mm long, moderately attenuate upward; pappus 4.5–5.5 mm long 69, **a. typica**
 Outer involucreal bracts $\frac{1}{4}$ as long as inner bracts; achenes 5.5 mm long, strongly attenuate near apex; pappus 5–6.5 mm long 69, **b. meletonis**

69, **a. *Crepis bupleurifolia typica*** subsp. nov. Planta 3–6.5 dm alta; folia caudicalia lyrata regulariter pinnata; caulis superne ramosus; involucrea obconica, squamis exterioribus comparate longis; corolla interdum 16 mm longa, tubo 5–6 mm longo; antherae 5.5 mm longae, appendicibus 0.9 mm longis, filamentis brevis; achaenia 6.5 mm longa; pappus 4.5–5.5 mm longus.

Plant 3–6.5 dm high; caudical leaves lyrate, regularly pinnate, terminal segment ovate, hastate; cauline leaves oblanceolate-acute to lanceolate-acuminate; stem branched above middle, branches rather short, paniculate-corymbiform; outer involucreal bracts $\frac{1}{3}$ – $\frac{1}{2}$ as long as inner bracts; receptacle alveolate-fimbriate,



Fig. 111. *Crepis bupleurifolia typica*, a-g, from Kotschy in 1859 (MW); h, i, from Sintenis 3321 (Lund): a, part of plant, $\times \frac{1}{2}$; b, head before anthesis, $\times 2$; c, inner involucre bracts, outer face, $\times 4$; d, immature achene with pappus, $\times 8$; e, floret with pappus removed, $\times 4$; e', detail of ligule teeth, $\times 25$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, i, mature achene and pappus seta, $\times 8$.

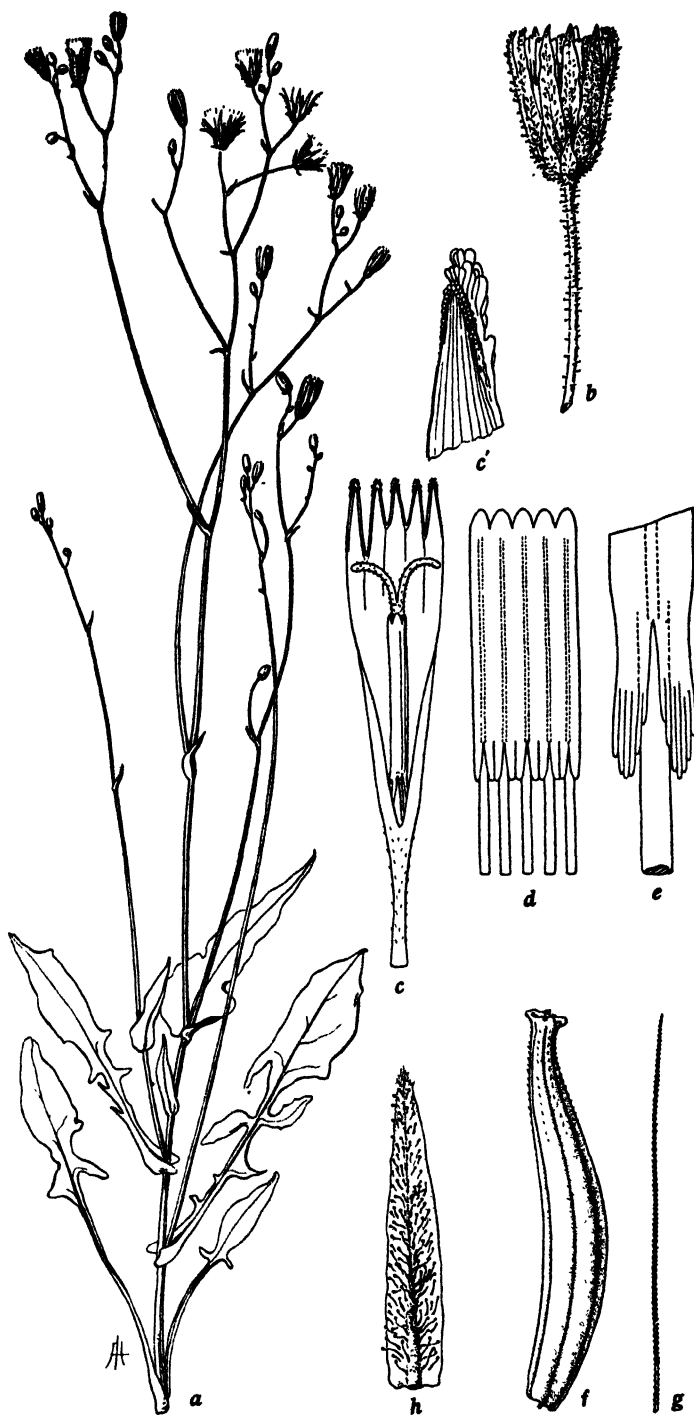


Fig. 112. *Crepis bupleurifolia meletonis*, from type (MW) and isotype (UWG): a, plant, $\times \frac{1}{2}$; b, young head, $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule teeth, $\times 25$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, g, achene and a pappus seta, $\times 8$; h, inner involucre bract, outer face, $\times 4$.

fimbriellae low, fleshy, naked; ligule in marginal florets 2.5 mm wide; teeth 1.4–1.8 mm long; corolla tube 5–6 mm long; anther tube 5.5×1.5 mm dis.; appendages 0.9 mm long, oblong, acute; filaments 0.4–0.6 mm longer; style branches attenuate; achenes 6.5 mm long, 1.3 mm wide, 5-costate, costae 3-ribbed, middle rib stronger, prominently thickened at base; pappus 4.5–5.5 mm long. See fig. 111.

Sonchus bupleurifolius Boiss. et Kotschy, ex Boiss., Fl. Orien. 3: 797. 1875.

Crepis bupleurifolia Freyn et Sint., loc. cit.

W. Kurdistan: Alischeri Khan (= Alischehir Dag, northeast of Marash †), meadows, 1878 m, Kotschy in 1859 (MW, UCf) type. **W. Armenia:** Erzerum Prov., Sipikor (25 km north of Erzingan) near Orumserai, *Sintenis 3321* (Lund, UCf).

69, b. ***Crepis bupleurifolia meletonis*** (Hand.-Mazz.) comb. nov. Plant 4–5 dm high; caudical leaves lyrate, irregularly pinnate, terminal segment oblong, hastate; cauline leaves lanceolate, acuminate; stem branched from near base upward, lower branches long, paniculately branched, upper branches shorter, subcorymbiform; outer bracts $\frac{1}{4}$ as long as inner bracts; receptacle (?); ligule in marginal florets 3 mm wide; teeth 1.5–2.5 mm long; corolla tube 4.5 mm long; anther tube 6×1.75 mm dis.; appendages 0.6 mm long, oblong, acute; filaments 1.25 mm longer; style branches 2.25 mm long, 0.2 mm wide, obtuse, yellow; achenes 5.5 mm long, 1 mm wide, 5-costate, costae rounded, striate or obscurely 3-ribbed; pappus 5–6.5 mm long. See fig. 112.

Crepis meletonis Hand.-Mazz., Ann. Naturhist. Hofmus. Wien, 27: 458. 1913.

Kurdistan: west of Bitlis, Meleto (Meretug) Dag, N. slope of peak among calcareous rocks, 2750 m, *Handel-Mazzetti 2830* (MW, UWG, UCf) type, isotype.

Relationship

Crepis bupleurifolia is probably closer to *C. Aitchisoni* of Afghanistan (q.v.) than to *C. willemetoides*, the species mentioned by Handel-Mazzetti, but it is very distinct from both. The former is even less known than *C. bupleurifolia*, but it has the same peculiar anther appendages which are revolute near the point of attachment to the filament and thus constrict the base of the anther tube. The achenes of *C. bupleurifolia*, with 5 major costae, each of which has 3 secondary ribs, are unique in *Crepis*. If *C. Aitchisoni* should be found to have achenes similar to those of *C. bupleurifolia*, there could be no question about the relationship of the two species, even though they differ greatly in habit. For the present, however, *C. Aitchisoni* is not sufficiently known to classify it satisfactorily. But *C. bupleurifolia* shows sufficient general resemblance to the species of this subsection to warrant including it here.

SUBSECTION D. SUBCORYMBIFORMAE

70. ***Crepis auriculaefolia*** Sieber

Ex Spreng., Syst. 3: 634. 1826. (Fig. 113.)

Perennial, 2–3.5 dm high; root strong, woody, slightly expanded at the base of the caudex; caudex 1–3 cm long, 0.8–1.5 cm wide, covered with brown bases of old leaves and at the crown with brownish grayish or whitish wool among the bases of the leaves; caudical leaves 6–21 cm long, 1.5–4.5 cm wide, oblanceolate or elliptic, obtuse-apiculate or -cuspidate, or acute, saliently denticulate or dentate, attenuate into a long or short winged petiole, \pm pubescent with pale glandless hairs, or glabrescent, or glabrous; cauline leaves reduced to lance-linear bracts; stem erect, terete, striate, glabrescent, tomentulose or puberulent, in early development heavily

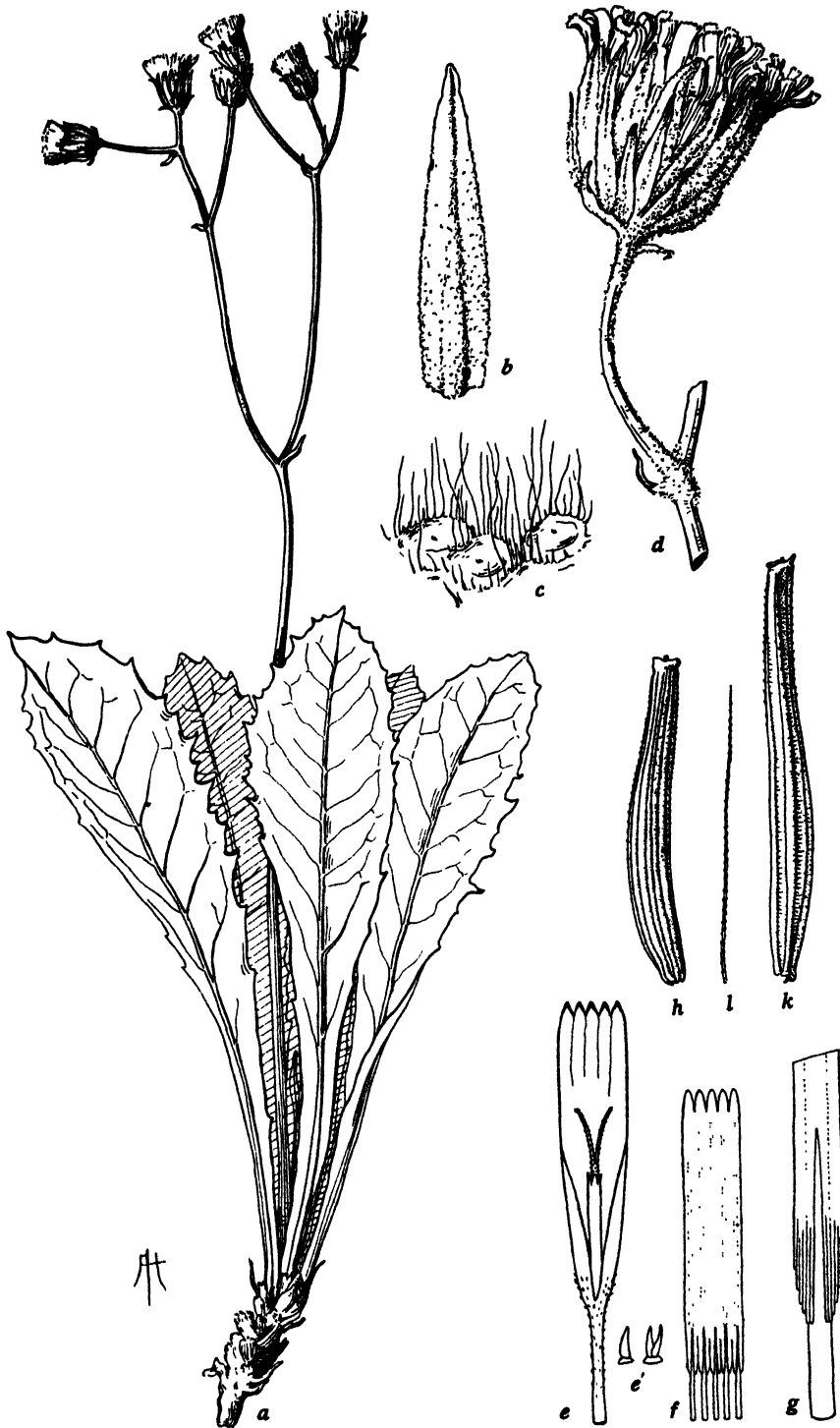


Fig. 113. *Crepis auriculaeifolia*, from Baldacci 233 (Mo 119415, 119419): a, plant, $\times \frac{1}{2}$; b, inner involucre bract from fruiting head, outer face, $\times 4$; c, detail of receptacle, $\times 16$; d, head with florets, $\times 2$; e, floret lacking ovary, $\times 4$; e', hairs on corolla tube, $\times 50$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, k, l, 2 achenes and a pappus seta, $\times 8$.

tomentose, sparsely woolly at the bifurcations, 2-3-branched near summit, forming a few-headed cymose-corymbiform inflorescence; peduncles 1-4 cm long, arcuate, 1-2-bracteate, tomentulose, scarcely thickened near the head; heads erect, medium, about 80-flowered; involucre campanulate, 10-14 mm high, about 8-10 mm wide at middle in fruit, \pm canescent-tomentose, occasionally pubescent with pale glandless hairs; outer bracts about 10, unequal, longest $\frac{1}{2}$ - $\frac{2}{3}$ as long as the inner, up to 2 mm wide, lanceolate, acute, often glabrescent, like inner ones darker in color toward the apex; inner bracts 14-18, up to 2.5 mm wide, lanceolate, acute or acuminate, densely strigulose on inner face with appressed white trichomes, becoming strongly carinate and spongy-thickened on lower half dorsally at full maturity; receptacle 4-5 mm wide, densely ciliate with several-celled trichomes 0.5-1.5 mm long; corolla about 14 mm long; ligule 2-2.5 mm wide; teeth 0.3-0.6 mm long; corolla tube 3.5-4.5 mm long, slender, beset with very short (less than 0.1 mm) stout single or double trichomes; anther tube 4.75×1 mm dis.; appendages 0.8 mm long, oblong, obliquely acute; filaments 0.75 mm longer; style branches 1.75 mm long, 0.1 mm wide, yellow; achenes stramineous, pale brown at summit, 5-6.5 mm long, 0.6-0.7 mm wide, obscurely or strongly 4-5-angled, the angles formed by the stronger ribs, with 3-5 weak striae between the ribs, gradually attenuate to the summit, slightly constricted below the scarcely expanded thin white pappus disk, narrowed at the unevenly calloused hollow base, strongly spiculate toward the summit; pappus white, 4.5-5.5 mm long, 1-2-seriate, the principal setae about equally fine, with a few extremely fine ones about 1 mm long, soft, deciduous. Flowering April-June; flowers yellow.

Hieraciodes auriculaefolium O. Kuntze, Gen. 1: 345. 1891.

Mountains of E. and W. Crete. Halacsy (Consp. Fl. Graec. 2: 216-231. 1902, sp. no. 4) states that it occurs at lower and montane elevations. Although no elevations are given by collectors, it is definitely said to occur in the vicinity of Kritsa, which is about 7 km from Mirabella Bay, at an elevation of about 600 m. Furthermore, Boissier (834) describes the location of one of Sieber's collections as "in faucibus montium Sphacioticorum," which would be interpreted by one familiar with that region as "in gorges of the mountains of Sphakia," and this would certainly indicate lower elevations. The upper limit of distribution of this species is not known, although there is one dubious record (*Gandoger 2704*) of 6200 ft. (1891 m); but in no place is it said to occur on or near mountain peaks, whereas its close relative, *C. Raulini*, is known to me only from alpine or subalpine elevations. It appears, therefore, that these two species occupy different altitudinal zones, although their areas may overlap.

Neither Sprengel (*loc. cit.*) nor de Candolle (172) cites any specimens; and no specimen exists in herb. DC. The only collection of Sieber mentioned by Boissier (*loc. cit.*) is the one mentioned above from the mountains of Sphakia, but this has not been seen by the present writer. However, another collection of Sieber from Mt. Dicta (Mo 119418) has been accepted by me as the type specimen.

Monomorphic.

Crete: *Lasithi Mts.*, Mt. Dicta, *Sieber* (Mo, type, Mu); *ibid.*, Aphendi Kristo, *Baldacci 233*, *Gandoger 2704* (Mo, UCf); *ibid.*, Mt. Aphendi Sarakeno, fissures of rocks, *Baldacci 233b* (Mo); *Mirabella dist.*, Mt. Lazaro, *Baldacci 233* (Bur); *ibid.*, on rocks in a gorge opposite Kritsa, *Heldreich 1435*, rocks above Kritsa, *Heldreich* in 1846 (Bo, UCf); *ibid.*, Critza Eparch, *Heldreich* in 1846 (Bur); *Lasithi Mts.*, *Guiol 2146* (UC).

Relationship

Crepis auriculaefolia has the most primitive type of achenes of any species in this subsection, even though its heads are not quite as large as those of *C. Baldacci* and

the inner involucreal bracts are more specialized by thickening. The florets are about the same size, but the anther tube and appendages are longer in *C. auriculaefolia*. Because of its occurrence as an endemic in Crete and because of its more primitive achenes, it may be inferred that *C. auriculaefolia* is actually an older species than *C. Baldaccii* and that its more specialized involucre has evolved under the influence of its xerophytic habitat. *C. auriculaefolia* is closely related to *C. Raulini* and less closely to the other Cretan endemic, *C. Sibthorpiana*, both of subsection E; it is also closely related to *C. Triasii* of this subsection. Since *C. Raulini* has 5 pairs of chromosomes, it may be assumed that *C. auriculaefolia* has the same number, but possibly a more primitive karyotype.

71. *Crepis Baldaccii* Hal.

Verh. zööl. bot. Ges. Wien, 42: 577. 1892 (1893). (Fig. 114.)

Perennial, 1.3–3.5, mostly 2–2.5, dm high; root strong, woody, crowned with the swollen caudex; caudex 0.5–2.5 cm wide, simple or divided, covered with brown bases of old leaves; caudical leaves 10–23 cm long, 2–4.5 cm wide, oblanceolate, acute or obtuse, retrorsely or runcinately dentate, or pinnately lobed with broad triangular acute dentate segments, or lyrate with a large denticulate or dentate terminal segment and a few mostly small lanceolate lateral segments, gradually reduced into a narrowly winged petiole usually shorter than the blade, finely pubescent with short pale gland hairs; cauline leaves, 1–4, similar or sessile, lanceolate, acuminate, with additional uppermost bractlike ones; stems 1–3, erect, terete, striate, puberulent or glabrescent, cymosely 1–4-furcate, the first bifurcation often near the base, branches strict, 1–2-headed; peduncles 1–10 cm long, rather stout, not thickened at base of head, tomentulose or tomentose and \pm gland-pubescent; heads erect, medium to large, 60–70-flowered; involucre broadly campanulate, 9–12 mm high, 7–10 mm wide at middle in fruit, canescent- or fuscous-tomentose or -tomentulose and densely gland-pubescent; outer bracts dark green, 10–14(18), very unequal, the longest $\frac{2}{3}$ – $\frac{3}{4}$ as long as the inner, lanceolate, acuminate; inner bracts 14–20, lanceolate, acuminate, silky-pubescent on both faces toward apex, glabrous and strongly nerved toward base on inner face, becoming slightly carinate and spongy-thickened dorsally at the very base at full maturity; receptacle 4–5 mm wide, alveolate, the fimbrillae membranous and densely ciliate with many short and a few longer shining trichomes, the latter up to 1.5 mm long; corolla 14–15 mm long; ligule 2 mm wide; teeth 0.3–0.5 mm long; corolla tube about 5 mm long, sparsely pubescent near the summit, with very short acicular hairs; anther tube about 4 \cdot 1.25 mm dis.; appendages 0.4 mm long, acute; filaments 0.75 mm longer; style branches 2.5 mm long, about 0.1 mm wide, yellow; achenes brown, 5–6.5 mm long, 0.6–0.8 mm wide, curved or straight, fusiform, gradually attenuate to the summit which is about 0.3 mm wide, with slightly expanded white pappus disk, narrowed at the strongly calloused yellow hollow base, about 20-ribbed, the ribs unequal, every fourth or fifth rib stronger, ribs close, narrow, rounded, muriculate under lens; pappus white, 8 mm long, 2-seriate, nearly equally fine, the coarsest about 50 μ (9 cells) wide at base, stiff but pliable, persistent. Flowering July–Aug.; flowers yellow. Chromosomes, $2n = 10$.

Endemic in Albania and N.W. Greece, in mountains from middle to highest altitudes, 1750–2350 m, on steep slopes in crevices of rocks.

Monomorphic.

Albania: Mt. Tomor (near Berat), the peak of Maja Tomorit, 2350 m, alpine, *Baldacci* 209 in 1892 (UWH type, UCF, K, Mu, Rome); ex hort. genet. Calif. 3417–1, grown from seed collected by Alston and Sandwith, no. K1662, at the type locality (UC); Mt. Cika (Delvino dist.,



Fig. 114. *Crepis Baldaccii*, *a-g*, from type (UWH) and isotypes; *h-j*, from *Baldacci 813* (Mo); *k*, from hort. genet. Calif. 3417 (grown from seeds collected at type locality, *Alston and Sandwith K 6612*): *a*, part of plant with young heads, $\times \frac{1}{2}$; *b*, stem and mature heads, $\times \frac{1}{2}$; *c*, mature head, $\times 2$; *d*, inner involucral bracts and part of receptacle, $\times 4$; *e-g*, 2 achenes and a pappus seta, $\times 8$; *h*, floret lacking ovary, $\times 4$; *i*, anther tube, $\times 8$; *j*, detail of appendages, $\times 32$; *k*, somatic chromosomes, $n = 5$, $\times 1250$.

south of Valona) mid-region, *Baldacci* 144 in 1894 (K, P, Bur, Fl, Mo); N. Albanian Alps, north of Abata, upper half of Bjeshka Madhë, 1750 m, *Dörfler* 262 (UWG, DL). Greece: Epirus, Mt. "Papington," Konitza dist. (probably Mt. Smolika), *Baldacci* 183 in 1896 (Bur, P, Mo); Mt. Smolika (near Konitza), *Guiol* in 1931 (UC).

Relationship

Crepis Baldaccii, next to *C. auriculaefolia*, is the most primitive species in this subsection, judging from size of flower heads, number and size of outer involucre bracts, and the limited amount of dorsal thickening of the inner bracts. Its karyotype is also primitive, since it resembles rather closely that of *C. pontana*. *C. Baldaccii* finds its closest relatives in *C. albanica* and the other Balkan members of this section, although it also shows affinity with *C. auriculaefolia* and *C. Raulini* as well as with *C. Triasii* and *C. macropus*.

72. *Crepis turcica* Degen et Baldacci

Ex Degen, Oestr. Bot. Zeitschr. 46: 417. 1896. (Fig. 115.)

Perennial, 2–5 dm high; root woody, about 7 mm wide at summit; caudex about 1.5 cm wide, covered with soft brown bases of old leaves; caudical leaves 8–16 cm long, 2–3 cm wide, oblanceolate, acute or obtuse, acutely runcinately dentate or pinnatifid, lobes and teeth mucronate, attenuate into a short or long winged petiole, with prominent pale midrib, \pm canescent-tomentulose, sometimes finely gland-pubescent on the lower face; cauline leaves small, lance-linear, acuminate, auriculate-amplexicaul, uppermost bractlike; stem erect, robust, terete, striate, puberulent below, tomentulose above, especially near the bifurcations, remotely 3–5-branched from near the middle or lower, branches cymose-paniculate, divaricate or rather strict, aggregate inflorescence corymbiform, 5–30-headed; peduncles 1–5 cm long, stout, straight or arcuate, several-bracteate, slightly constricted just below the head; heads erect, medium, about 70-flowered; involucre campanulate, 11–12 mm high, 7–8 mm wide in fruit, canescent-tomentulose to densely white-woolly; outer bracts 6–8, with several lax subtending ones, the longest $\frac{1}{2}$ as long as the inner, linear, dark at the apex; inner bracts 12–16, lanceolate, acute, dark at the apex, silky-pubescent on inner face, becoming dorsally strongly carinate and brown spongy-thickened beginning with anthesis; receptacle alveolate, fimbriae low, ciliate with fine soft white hairs up to 1 mm long; corolla about 15 mm long; ligule 2.3–2.6 mm wide; teeth about 0.5 mm long; corolla tube about 4 mm long, pubescent with stout several-celled hairs 0.05–0.4 mm long; anther tube 4.5×1.2 mm dis.; appendages 0.6 mm long, obliquely acute; filaments 1 mm longer; style branches about 2 mm long, 0.1 mm wide, yellow; achenes brown, 4–5 mm long, 0.6–0.8 mm wide, subterete or somewhat angled, slightly attenuate to both ends, without an expanded pappus disk, yellow at the nearly closed small calloused base, 10–12-ribbed, ribs rather wide, sometimes with 3 stronger ones, rounded, finely spiculate at the apex; pappus white, 5 mm long, 2-seriate, very fine, soft, deciduous. Flowering June–July; flowers yellow.

N.W. Greece and the Albanian frontier at low montane elevations (probably about 1000 m) in rocky places. Known to me from only 3 collections.

The place where the type (*Baldacci* 323) is deposited is not known to the present writer. It may be in the Herbarium of the University of Vienna, but when I applied for a photograph of the type I received a picture of a sheet of *Baldacci* 182, of which collection I have seen several specimens elsewhere. I saw a specimen of No. 323 in the Burnat herbarium, however, and have assumed that it is a duplicate of the type rather than the type itself.

This is a rather variable species in respect to the habit of branching (cf. fig. 115).



Fig. 115. *Crepis turcica*, a-n, from Baldacci 182 (Mo 119556, except h, i, in Fl): a, flowering plant, many-headed variant, $\times \frac{1}{2}$; b, fruiting plant, few-headed variant, $\times \frac{1}{2}$; c, mature head, $\times 2$; d, e, inner involucre bract, inner and outer faces, $\times 4$; f-i, 2 achenes and pappus setae, $\times 8$; k, detail of receptacle, $\times 25$; l, floret lacking ovary, $\times 4$; m, anther tube, $\times 8$; n, detail of appendages, $\times 32$.

The branches may be strict and 1-2-headed or divaricate and 2-9-headed. There is considerable variation in the amount of tomentum on the involucre; in some plants it is very dense and feltlike. The leaves also may have much or little tomentum, and gland hairs may be present on the lower side of the leaves or entirely absent. The achenes of different plants vary in the regularity of the width of the ribs. But all of this variation is in degree of expression of the same characters. The species, as it is known from the limited collections thus far made, is very distinct from all the other members of this section.

Greece: Epirus, Malakasion dist., Kalarrytai, near Arta R., among rocks, *Baldacci 323* in 1895 (Bur, isotype). **Albania or Greece (†):** Ljaskovik (Leshkovik) dist., Mt. Prophitis Ilias and Kuruna, above Vonieko, *Baldacci 182* in 1896 (Bur, K, UWG, UWH, P, Fl, Mo, UCf). Further data on the distribution of this species are given: (1) by Halacsy (Consp. Fl. Graec. 2: 216-231. 1902, sp. no. 5), who states that the type collection came from the base of Mt. Peristeri, near Kalarrytai; and (2) by Markgraf (*in litt.*), quoting from Baldacci (N. Giorn. Bot. Ital., n. ser. 6: 186. 1899), who states that another collection was made on the mid-region of Mt. Vradeton (Greece, Epirus) Zagorion dist., above Cepelovon.

Relationship

Crepis turcica appears to be closest to *C. albanica*, from which it is very distinct in the 1-stemmed caudex, less deeply pinnatifid leaves, subcorymbiform inflorescence, narrower outer involucre bracts and fewer, wider ligules, and especially the shorter, less attenuate, unequally ribbed achenes and shorter, finer pappus. It is noteworthy also that the pale appearance of the basal part of the involucre in *C. albanica* is due not to tomentum but to the whitish surface of the greatly thickened bracts, whereas in *C. turcica* the pale aspect is due to tomentum which is sometimes thick and feltlike. Although the involucre in *C. turcica* is considerably less primitive in type than that of *C. Pantocsekii*, the unequally ribbed achenes of *C. turcica* are definitely more primitive.

73. *Crepis Pantocsekii* (Vis.) Markg.

Fl. Pen. Balcan, Rept. Beih. 30 (2): 851. 1931. (Fig. 116.)

Perennial, 3-5 dm high; root very slender, woody; caudex \pm swollen, very leafy; caudical leaves 10-18 cm long, up to 4 cm wide, erect, oblanceolate, acute or acuminate, pinnately parted almost to midrib, with narrow terminal segment and numerous narrow acuminate dentate lateral segments, strongly attenuate into a narrow petiole, becoming gradually broadened to the conspicuous scarious imbricate base, glaucescent beneath, like stems canescent-tomentulose with fine white mostly glandless hairs; cauline leaves few, reduced, pinnatifid, entire or bractlike; stems 1-3, erect, slender, terete, simple or 1-3-furcate, the first bifurcation near the middle, branches 1-2-headed; peduncles 3-16 cm long, erect, slender, becoming sulcate and slightly thickened near head in fruit, tomentulose or tomentose and gland-pubescent near head; heads erect, medium, about 50-flowered; involucre campanulate, 10-13 mm high, 6-8 mm wide, canescent-tomentose, gland-pubescent, glands brown; outer bracts 14-18, very unequal, longest $\frac{2}{3}$ - $\frac{3}{4}$ as long as inner ones, lanceolate, acuminate, outermost lax; inner bracts 14-18, nearly equal, lanceolate, acuminate, ciliate at apex, pubescent on inner face, becoming carinate and spongy-thickened near base in fruit; receptacle alveolate-fimbrillate, fimbrillae densely white-ciliate; corolla 13.5 mm long; ligule 2.25 mm wide; teeth 0.3-0.6 mm long; corolla tube 4.5 mm long, pubescent with coarse acicular hairs up to 0.6 mm long; anther tube 4×1.25 mm dis.; appendages 0.8 mm long, lanceolate, acuminate; filaments 0.75 mm longer; style branches 1.5 mm long, 0.15 mm wide, yellow; achenes brown, about 6 mm long, fusiform, strongly attenuate toward apex, constricted at

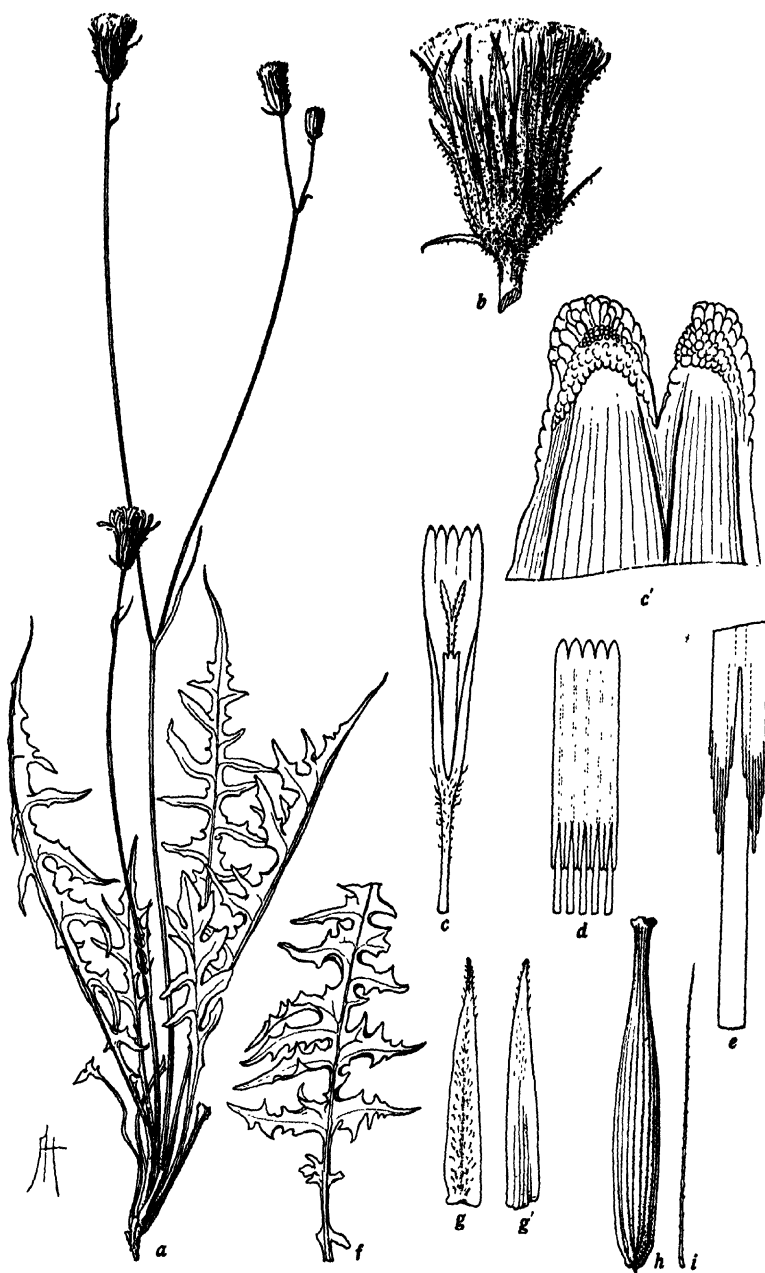


Fig. 116. *Crepis Pantocsekii*, *a-c*, from Pichler in 1868 (Bo); *f-i*, from Pichler in 1885 (Genoa): *a*, plant, $\times \frac{1}{2}$; *b*, head, post anthesis, $\times 2$; *c*, floret lacking ovary, $\times 4$; *c'*, detail of ligule teeth, $\times 50$; *d*, anther tube, $\times 8$; *e*, detail of appendages, $\times 32$; *f*, caudical leaf, $\times 1$; *g*, *g'*, inner involucre bract, outer and inner faces, $\times 4$; *h*, *i*, achene and pappus seta, $\times 8$.

the hollow calloused base, 16–18-ribbed, ribs narrow, rounded, smooth or finely spiculate near the apex; pappus yellowish-white, 6 mm long, 2-seriate, rather coarse, brittle, united at base, persistent, slightly exceeding the involucre. Flowering June; flowers yellow.

Gatyona Dioscoridis var. ♀ *glandulosa* Griseb., ex Pant., Adnot. 48. 1870.

Crepis alpestris (Jacq.) Tsch. var. *moesiaca* Aschs. et Huter, Oest. Bot. Zeitschr. 19: 67. 1869.

Gatyona Pantocsekii Vis., Fl. Dalm. Suppl. alterum pars, 2: 53, t. 5. 1881.

Crepis moesiaca Degen et Baldacci, ex Degen, Oest. Bot. Zeitschr. 44: 302. 1894.

Crepis Vandasii Rohl., Sitz. Böhm. Ges. Wiss. No. 38: 66. 1904.

Crepis moesiaca Aschs. et Huter, Oest. Bot. Zeitschr. 57: 112. 1907.

Crepis adenantha Pichler, ex Degen, *loc. cit.*, *nomen*.

Yugoslavia, in the mountains of Dalmatia, Bosnia, Hercegovina, Montenegro, and Serbia, from 900 to 1500 m alt., often on calcareous rocks.

Although the type of Visiana has not been seen by me, his illustration (*loc. cit.*) agrees closely with specimens of Huter, Pichler, and Rohlena, which are cited below.

Monomorphic.

Dalmatia: Mt. Orjen, 909 m, *Huter* in 1867 (UWII); Cattaro dist., near Cerkojia, *Huter* in 1867 (K); near Cerquizzo, *Pichler* in 1870 (Kerner, K); Crivarje Baiche, above Orai havai, *Pichler* in 1885 (K, Genoa, Ucf). **Montenegro:** Mt. Lovćen, *Pichler* in 1868–1870 (Bo, Ucf, K, Bur); Piva, near Borkovici, *Rohlena* in 1905 (Bur).

Relationship

Crepis Pantocsekii is closest to *C. Baldaccii*, from which it is very distinct in the acuminate leaves, taller, more slender stem, smaller heads, with narrow acuminate involucreal bracts, longer, acuminate anther appendages, strongly attenuate achenes, and shorter pappus slightly exceeding the involucre. The statement of Rohlena (*loc. cit.*) that *C. Pantocsekii* is closely related to *C. athoa* is based on superficial resemblance. *C. Pantocsekii* and *C. Baldaccii* show most affinity with *C. turcica* and *C. albanica*.

74. *Crepis Triasii* (Camb.) Fries

Nova Acta Reg. Soc. Sci. Upsala, ser. 2, 14: 220. 1848. (Fig. 117.)

Perennial, 1–4.5 dm high; root slender, woody; caudex straight or oblique, brown, woody, 5–8 mm wide, simple or bifurcate, brown-woolly at bases of leaves; caudical leaves numerous, up to 13 cm long, 3.5 cm wide, rarely 23 cm long, oblanceolate, obtuse or acute, attenuate into a winged petiole with clasping base, denticulate to coarsely dentate, teeth acute, rarely pinnately shallow-lobed, lobes acute or rounded, obtuse, pubescent on both sides with fine pale yellow glandless hairs; cauline leaves few, lower ones similar to caudical leaves or sessile, uppermost small, bractlike; stems 1–3, ascending, flexuous, terete, striate, not fistulose, canescent-tomentulose, tomentose at bifurcations, 2–4-furcate, aggregate inflorescence cymose-corymbiform; peduncles 0.5–6(8) cm long, slender, not thickened near base of head in fruit, ± tomentose, often 1-bracteate; heads erect, medium or large, up to 70-flowered; involucre campanulate, 10–12 mm high, 5–7 mm wide in anthesis, like peduncle canescent-tomentose; outer bracts 10–13 in 2 ranks, nearly equal, longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner bracts, linear, acute, conspicuously spreading, like inner bracts sometimes pubescent with pale yellow or greenish glandless hairs; inner bracts 10–16, lanceolate, acute, ventrally glabrous, dorsally keeled in fruit, conspicuously spongy-thickened and confluent at base, sometimes ultimately reflexed; receptacle flat, areolate-fimbriate, fimbriae ciliate with white hairs up to 0.5 mm long; corolla 12–13 mm long; ligule 2.5–2.75 mm wide; teeth about 0.5 mm long, broadly triangular; corolla tube 3 mm long, 0.4 mm wide, cylindric, stout,

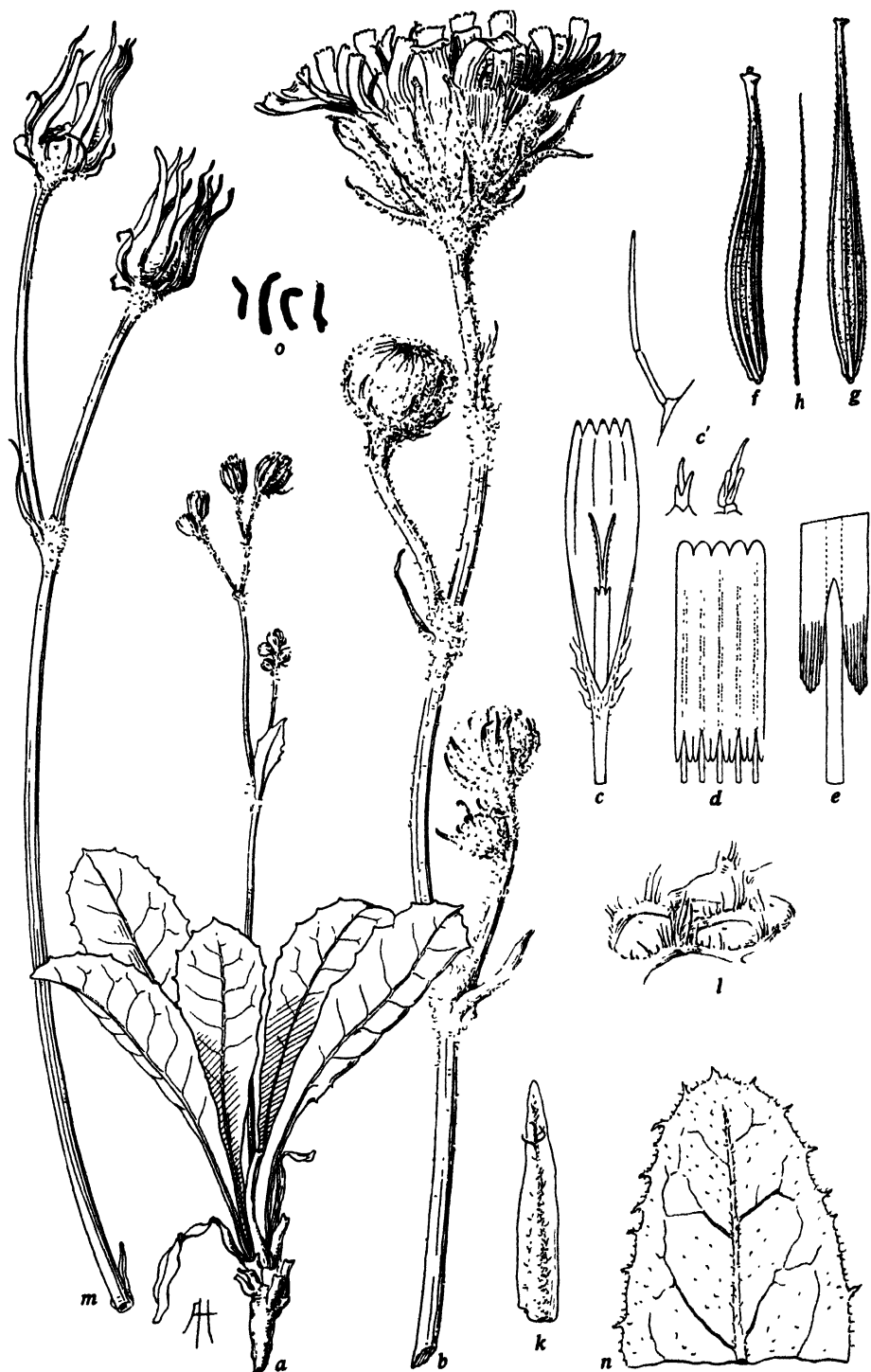


Fig. 117. *Crepis Triasii*, a, authentic spec. (K); b-e, from Rodriguez in 1872 (F1); f-k, from Bianor in 1911 (Bur); l-o, from Babcock 380 (UC 429419): a, plant, $\times \frac{1}{2}$; b, part of inflorescence with 4 heads, $\times 2$; c, floret lacking ovary, $\times 4$; c', hairs on corolla tube, $\times 50$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f-h, 2 achenes and a pappus seta, $\times 8$; i, inner involucre bract, outer face, $\times 4$; j, detail of receptacle, $\times 16$; k, 2 old heads, $\times 2$; l, upper $\frac{1}{4}$ of a young leaf, $\times 2$; m, somatic chromosomes, $n = 4$, $\times 1250$.

beset with long and short trichomes, short ones 0.1–0.2 mm long, simple or 2–3-parted, long ones 0.5–0.7 mm, several celled; anther tube 3.75×1.5 mm dis., yellow; appendages 0.5 mm long, obtuse; filaments 0.3 mm longer; style branches 1.6 mm long, 0.2 mm wide at base, gradually attenuate, yellow; achenes all very dark brown, 5.5–8.5 mm long, 0.75 mm wide, fusiform, attenuate into a definite beak 1–3 mm long, with expanded pappus disk, shortly attenuate to the yellow calloused sometimes oblique base, 10-ribbed, ribs rounded, densely and finely spiculate; pappus white, 4–5.5 mm long, 1-seriate, fine, soft, persistent. Flowering April–July; flowers bright yellow. Chromosomes, $2n = 8$.

Hieracium Triasii Camb., Enum. Pl. Ins. Balear, 91. 1827.

Barkhausia balearica Costa, Ind. Sem. Hort. Barcin., 1861.

Crepis balearica Costa, Fl. Catal., 153. 1864.

Hieraciodes Triasii O. Kuntze, Gen. 1: 346. 1891.

Spain, Balearic Islands, endemic. Common in Majorca throughout the N. mountains from 60 to 1000 m alt., in crevices of rocks, on moist banks, and on moss-covered walls. Rare in Minorca (in S. "barrañicos," 10–1000 m, acc. to Knoche, Fl. Bal. 2. 1922).

Majorca: "Cambess. dedit Feb. 1827" ex. herb. J. Gay, (K) type; without definite locality, Ball in 1844 sub *Crepis* (K); Ermila, sides and fissures of rocks, Mares in 1852 (K); without definite locality, Bourgeau in 1869 (US); between Palma and Valldemosa, near Valldemosa, Burnat in 1881 (Bur) m.v. 1; Mt. Puig de Galatzo and Mt. Comun, above Bañola, calcareous rocks, 800–1000 m, Porta et Rigo in 1885 (MW) m.v. 2; El Feix, Gros in 1920 (Bar); Lluch, Gros in 1920 (Bar); Coll del Coloms, Gros in 1920 (Bar); Arta, Penyal de les muntanyes, L. G. Font (Bar); Soller, calcareous rocks, Font Quer in 1920 (Bar); crevices of rocks around Soller, 100–1000 m, Bianor in 1911 (Bur); rocks at 1000 m, Knoche 210 (Ms); above Barañica de Soller, on rocks at base of cliffs along main crest, Babcock 380 (UC) and Babcock 380–2 (UC) m.v. 3; between Miramar and Valldemosa, in moss on wall near spring in deep shade, about 250 m, Babcock 385 (UC) m.v. 4; Salt d'es Ca, Gros in 1920 (Bar) m.v. 5. **Minorca:** Santa Poriza, calcareous rocks, Rodriguez in 1872 (Fl); Santa Ponza de Alayor, Peñas col, Font Quer in 1917 (Bar, UC); Deya Vell, Guerau in 1903 (Bar).

Minor Variants of *C. Triasii*

1. Achenes scarcely beaked though strongly attenuate at summit. Possibly a more primitive form of the species. Burnat in 1881 (Bur), near Valldemosa, between Valldemosa and Palma, Majorca.

2. Leaves up to 18 cm long; outer involucre bracts 7–11 mm long. Probably a shade form. Porta et Rigo in 1885 (MW), on rocks, Mt. Puig de Galatzo and Mt. Comun, above Bañola, Majorca.

3. Leaves pinnately shallow-lobed, lobes rounded, obtuse. One of 12 plants grown in hort. genet. Calif. from original roots, Babcock 380 (UC), on rocks at base of cliffs along main crest above Barañica de Soller, Majorca.

4. Leaves up to 23 cm long, coarsely dentate, teeth triangular, acute; heads rather small. Shade form. Babcock 385 (UC), in moist moss on a wall in deep shade, between Miramar and Valldemosa, Majorca.

5. Much reduced; leaves up to 6 cm long; stem, including head, up to 9 cm long, scapiform, with one or two small abortive heads. Gros in 1920 (Bar), Salt d'es Ca, Majorca.

Relationship

In its large, nearly entire petiolate leaves *Crepis Triasii* shows considerable resemblance to *C. auriculaefolia* and *C. Raulini*, and it resembles the former in habit; but the 2 Cretan endemics differ from *C. Triasii* in many characters. Yet the resemblances noted are sufficient to suggest that these 3 species represent early departures from a very old *Crepis* stock. *C. auriculaefolia*, however, is much more primitive in its less specialized involucre and achenes; and it may safely be assumed that its karyotype is somewhat similar to that of *C. Raulini*. But *C. Triasii* shows considerable resemblance to *C. vesicaria* and its allies in its chromosomes, as

well as in its specialized involucre and definitely beaked achenes. Hence, it may be considered as the most advanced species in this subsection and as a connecting link between this section and sec. 25.

SUBSECTION E. DIVARICATAE

75. *Crepis Raulini* Boiss.

Diag. Pl. Or. Nov. ser. 1, 11: 58. 1849. (Fig. 118.)

Perennial, 0.6–1.5 dm high; root long, slender, woody, crowned with the expanded caudex; caudex 1–3 cm wide, simple or divided, covered with brown bases of old leaves, densely white or yellowish-woolly among the bases of the leaves; caudical leaves numerous, 3–8 cm long, 1–3 cm wide, obovate or oblanceolate, acute or obtuse, denticulate to coarsely runcinate-dentate, attenuate into a very short broadly winged petiole, or the petiole sometimes elongated and narrowly winged, pubescent on both sides with short pale gland hairs, white-woolly at the very base; cauline leaves reduced to linear bracts at the bifurcations of the stem; stem erect, slender, terete, striate, dichotomously 1–2-furcate, the branches divaricate, or sometimes subcorymbiform in habit of branching, white-woolly at the bifurcations; peduncles 1.5–7 cm long, slender, slightly thickened near the head, canescent-tomentulose, sometimes sparsely gland-pubescent, often 1–2-bracteate; heads erect, medium, 50–70-flowered; involucre yellowish or brownish-green, cylindric-campanulate, 10–11 mm long, 4–6 mm wide at middle in fruit, canescent-tomentose, sparsely gland-pubescent, and sometimes sparsely setose with long pale glandless setae; outer bracts 6–8, sometimes with 1–4 subtending ones, unequal, longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner in fruiting heads, up to 0.8 mm wide, lance-linear, acute; inner bracts 12–20, lanceolate, 1–1.5 or rarely 2 mm wide, acute or acuminate, finely pubescent on inner face with appressed shining hairs, becoming strongly carinate and spongy-thickened confluent with the base at full maturity; receptacle 3–4 mm wide, areolate, densely ciliate with white trichomes 0.5 mm long; corolla in marginal florets about 14 mm long; ligule 2.25 mm wide; teeth 0.5–1 mm long; corolla tube 4.5–5 mm long, slender, sparsely beset with very short (up to 0.15 mm long) single or double 1–3-celled stout trichomes; anther tube 4×1 mm dis.; appendages 0.8 mm long, oblong, acute; filaments 0.5 mm longer; style branches 2 mm long, 0.1 mm wide, yellow; achenes grayish-tawny, 5–6 mm long, 0.7–1.2 mm wide, subterete or angular, fusiform, definitely attenuate toward the apex, with scarcely or slightly expanded white pappus disk, somewhat narrowed toward the strongly calloused nearly closed base, about 20-ribbed, ribs very fine, with 3–5 definitely stronger ones, these forming the strong basal callosity, strongly spiculate on upper half; pappus white, 4–6 mm long, 1–2-seriate, fine, soft, deciduous. Flowering June; flowers yellow. Chromosomes, $2n = 10$.

Hieraciodes Raulini O. Kuntze Gen. 1: 346. 1891.

W. Crete, in the higher mountains, alpine. Except for the collections of Baldacci and Raulin (cf. Halacsy, Consp. Fl. Graec. 216. 1902) on Mt. Psiloriti, which is in the center of the island, this rare endemic species is known only from the W. part of the island.

Crete: without definite locality, *Raulin 354* in 1867 (Bo, UCf) type; Mylopotamos dist., Mt. Psiloriti, fissures of rocks above Jove's cave, *Baldacci 87* (Bur, Mo); Canea reg., White Mts., trail from Omalo Plateau to Mt. Volakia, near Linoselli spring, about 2000 m, exposed rocky slope, near patches of snow, on June 24, 1930, *Babcock 312* (UC); Canea reg., Mt. Hagion Pneuma (= Pnevma), about 10 km east of Mt. Volakia, June, 1932, *Guil 2185* (UC).

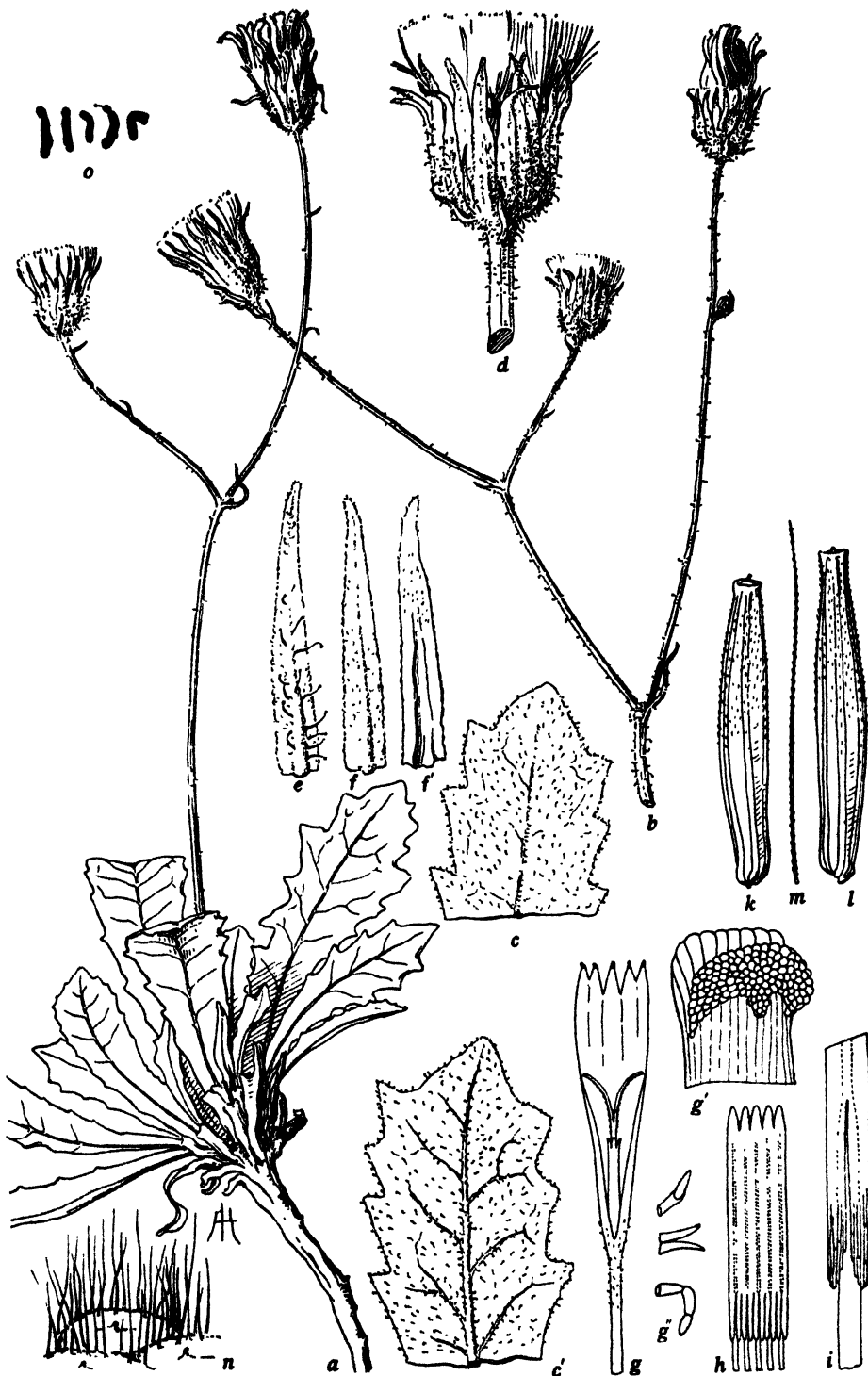


Fig. 118. *Crepis Raulini*, from Babcock 312 (UC 429359): a, plant, $\times 1$; b, 1 complete inflorescence, $\times 1$; c, c', upper and lower surfaces of caudical leaves, $\times 2$; d, nearly mature head, $\times 2$; e, inner involueral bract of outer series, outer face, $\times 4$; f, f', outer and inner faces of inner involueral bract, inner series, $\times 4$; g, floret lacking ovary, $\times 4$; g', detail of ligule tooth, $\times 50$; g'', details of hairs on corolla tube, $\times 50$; h, anther tube, $\times 8$; i, detail of appendages, $\times 32$; k-m, 2 achenes and a pappus seta, $\times 8$; n, detail of receptacle, $\times 25$; o, somatic chromosomes, $n = 5$, $\times 1250$.

Minor Variant of C. Raulini

1. (*C. Degenii* Bald. in herb.) Plant very small; caudical leaves 2.5 cm long, white-woolly at the base; stem scapiform, 1-headed, 5 cm high; leaves, stem, and involucre shortly gland-pubescent; immature achenes resemble those of *C. Raulini*; also the leaves are like those of this species in shape and the denticulate to dentate margins. The slender root is broken off, but the caudex is 1 cm wide, including the brown bases of old leaves. The locality given on the original label is illegible. Probably this is merely a reduced form which grew at an unusually high altitude, *Baldacci* 76 (Rome, UC) July 8, 1893, Crete.

Relationship

Crepis Raulini is closest to *C. auriculaefolia*, also of Crete, and next closest to *C. albanica*. From both it is very distinct in the low stature, the size and shape of the leaves, the glandular pubescence over the whole plant, the slender peduncles, and especially in the grayish-tawny strongly spiculate achenes. In stature and bract width it is a more reduced species than *C. auriculaefolia*; and its 5 pairs of chromosomes, although similar to those of *C. Baldaccii*, are all smaller. Pot-grown plants in a greenhouse maintained the distinctive features of the species.

76. *Crepis albanica* (Jav.) comb. nov.

(Fig. 119.)

Perennial, about 3.5 dm high; root strong, woody, indefinitely merging into the caudex; caudex elongated, 1-furcate, much enlarged and divided at the crown, which is covered with brown bases of old leaves; caudical leaves numerous, 10–15 cm long, 2.5–3 cm wide, oblanceolate, acute, deeply and irregularly runcinate-pinnatifid to lyrate-pinnate with large acutely dentate terminal lobe and acute rapidly reduced remote lateral lobes, attenuate into a narrow petiole often longer than the blade, sparsely puberulent or often glabrous; lower cauline leaves similar or sessile, middle ones lance-linear, acuminate, uppermost bractlike; stems 3–4 to a caudex, erect, terete, puberulent or glabrous, cymosely dichotomous, 1–3-furcate, the branches divaricate, 1–2-headed, the terminal two sometimes equally robust; peduncles 4.5–12 cm long, mostly bractless, tomentose and somewhat wider near the head; heads erect, medium, 70–80-flowered, involucre campanulate, 11–14 mm high, 7–9 mm wide at middle in fruit, when fully mature conspicuously pale at the base in contrast with the dark bracts, canescent tomentose and shortly gland-pubescent; outer bracts about 12, unequal, longest $\frac{2}{3}$ as long as the inner, lance-linear, acuminate; inner bracts about 18, lanceolate, acute or acuminate, with dark dorsal mid-region, pale or scarious at margin, densely silky-pubescent on upper half of inner face, becoming dorsally strongly carinate and pale spongy-thickened confluent with the swollen base; receptacle about 4 mm wide, alveolate, fimbriate membranous, shortly white-ciliate; corolla 18 mm long; ligule 1.5 mm wide; teeth 0.5 mm long; corolla tube 5 mm long, shortly pubescent near summit and on base of ligule; anther tube 5×1.2 mm dis.; appendages 0.75 mm long, oblong, obtuse; filaments 0.5 mm longer; style branches 2.75 mm long, yellow (?); achenes reddish-brown, fading to yellow at the summit, 6.5–7.75 mm long, 0.7–0.8 mm wide, gradually attenuate to the summit which is 0.3–0.4 mm wide, with slightly expanded pale pappus disk, narrowed or constricted at the brown-calloused oblique base, with a protruding yellow callosity, about 20-ribbed, the ribs nearly equal or 3–5 slightly stronger, narrow, close, rounded, finely spiculate under lens; pappus white, 7 mm long, 1-seriate, nearly equally fine, the coarsest setae about 50μ (6 cells) wide, rather stiff but pliable, persistent. Flowering July–Aug.; flowers yellow.

Crepis Baldaccii subsp. *albanica* Jav., Magy. Bot. Lap. 21: 21. 1923.

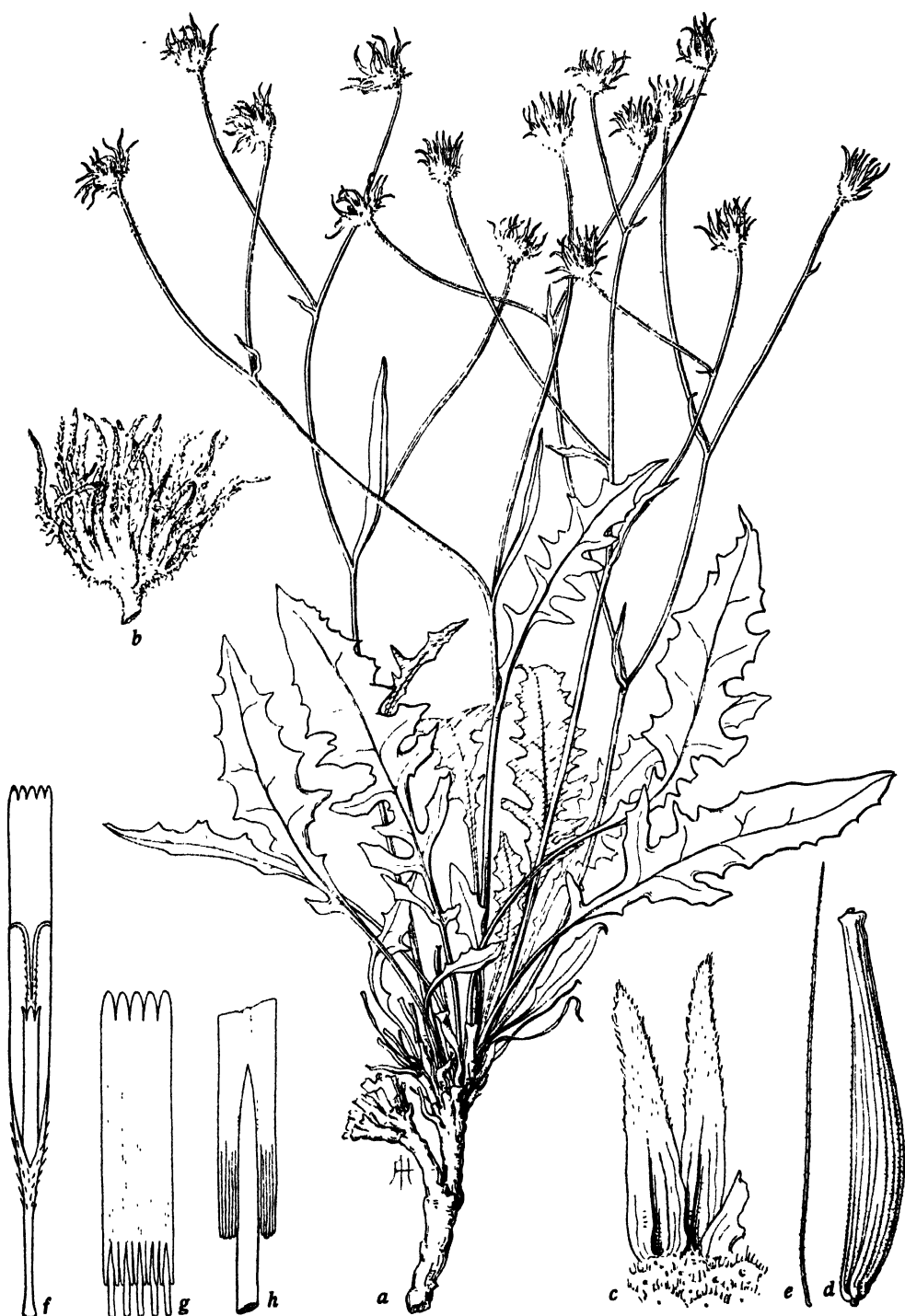


Fig. 119. *Crepis albanica*, from type (Budapest): a, part of plant, $\times \frac{1}{2}$; b, old head, $\times 2$; c, 2 inner involucral bracts, ventral face, and adjacent part of receptacle showing cilia on margins of the areoles, $\times 4$; d, e, achene and pappus seta, $\times 8$; f, floret lacking ovary, $\times 4$; g, anther tube, $\times 8$; h, detail of appendages, $\times 32$.

E. part of the N. Albanian Alps. Known with certainty from only one locality, which is now in Yugoslavia.

On the type sheet (no. 1 of the 4 folios in the Herbarium of the National Hungarian Museum) there is a fragmentary specimen of a plant which is almost certainly *C. Baldacci*. If this species actually occurs with *C. albanica*, we have here a new locality for the former.

Monomorphic.

Yugoslavia: N. Albanian Alps, E. part, Maja Hekurave, below Mt. Maja Droshkës, above the village of Dragobija, about 1400 m, in calcareous gravel, *Javorka*, Aug. 30, 1918 (Budapest, type UCf, K); Ipek dist., ravine or canyon opposite the town of Plav, *Csiki* in 1917 (Budapest), immature, but probably this species.

Relationship

Crepis albanica, although confused with *C. Baldacci* by Jávorka, is certainly distinct. This is particularly borne out by the unusually prominent spongy-thickened involucre in mature heads of *C. albanica*, as contrasted with the much less specialized involucre of *C. Baldacci*. In addition, there are well-marked differences in the flowers and fruits of the two species as well as in the habit of branching and in other characters. *C. albanica* is also related to *C. macropus*, and less closely to *C. Pantocekii* and *C. turcica*.

77. *Crepis macropus* Boiss. et Heldr.

Ex Boiss., *Diag. Pl. Or. Nov. ser. 1*, 11: 57. 1849. (Fig. 120.)

Perennial, 2.5–3.5 dm high; root woody, 4–5 mm wide; caudex 1–4 cm long, 1–2 cm wide at the leafy crown, covered below with brown bases of old leaves; caudical leaves 10–15 cm long, 1.5–3 cm wide, oblanceolate or lanceolate, acute, pinnately parted with close or remote lanceolate acute or acuminate segments, lobes entire, denticulate or strongly dentate, the lobes and teeth corneous-mucronate, attenuate into the narrowly winged petiole with broader base, conspicuously pale spongy-thickened toward the base, canescent-tomentulose, sparsely setulose along the veins especially on the lower face with pale glandless setae; lower cauline leaves similar or sessile, acuminate, the others linear or bractlike; stem erect, terete, tomentulose or glabrescent, sometimes sparsely setulose, divaricately remotely 2–5-branched usually from near the base, branches long, 1-headed, or divaricately 1–2-furcate, forming a broad open cymose-corymbiform aggregate inflorescence; peduncles 8–18 cm long, stiffly divaricate or arcuate, rather slender, glabrescent, 1–2-bracteate, definitely constricted, yellowish and tomentulose near the head; heads erect, medium, about 50-flowered; involucre campanulate, 11–13 mm long, 8–10 mm wide at middle when mature, densely canescent-tomentulose; outer bracts 8–12, with 1–3 subtending, unequal, the longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner, somewhat lax, linear, dark above, pale, scarious and somewhat thickened near the base; inner bracts 12–16, lanceolate, acute, dark and glabrescent near the white-ciliate apex, sometimes with a few median dorsal black setae near the apex, glabrous on inner face, becoming broadly carinate dorsally and somewhat spongy-thickened confluent with the base at maturity; receptacle alveolate, fimbriae dentate, finely white-ciliate, cilia about 1 mm long; corolla about 14 mm long; ligule 2 mm wide; teeth 0.5–0.75 mm long; corolla tube 4–5 mm long, pubescent with coarse several-celled hyaline hairs up to 0.3 mm long; anther tube 4×1.2 mm dis.; appendages 0.75 mm long, lanceolate, acute; filaments 0.6 mm longer; style branches 2–2.5 mm long, 0.15 mm wide, yellow; achenes reddish-brown, about 7 mm long, 0.7 mm wide, fusiform, gradually attenuate to the summit which is about 0.3 mm wide, with

definitely expanded greenish pappus disk, narrowed near the slightly calloused slightly closed base, 10-ribbed, ribs equal, rounded, muriculate under lens; pappus white, 8 mm long, 2-seriate, outer series finer, inner series up to 60μ (7 cells) wide at base, rather stiff but pliable, persistent. Flowering June; flowers yellow.

Crepis divaricata var. *longipes* Boiss. et Heldr., ex Boiss., loc. cit., as syn.

Hieraciodes macropus O. Kuntze, Gen. 1: 346. 1891.

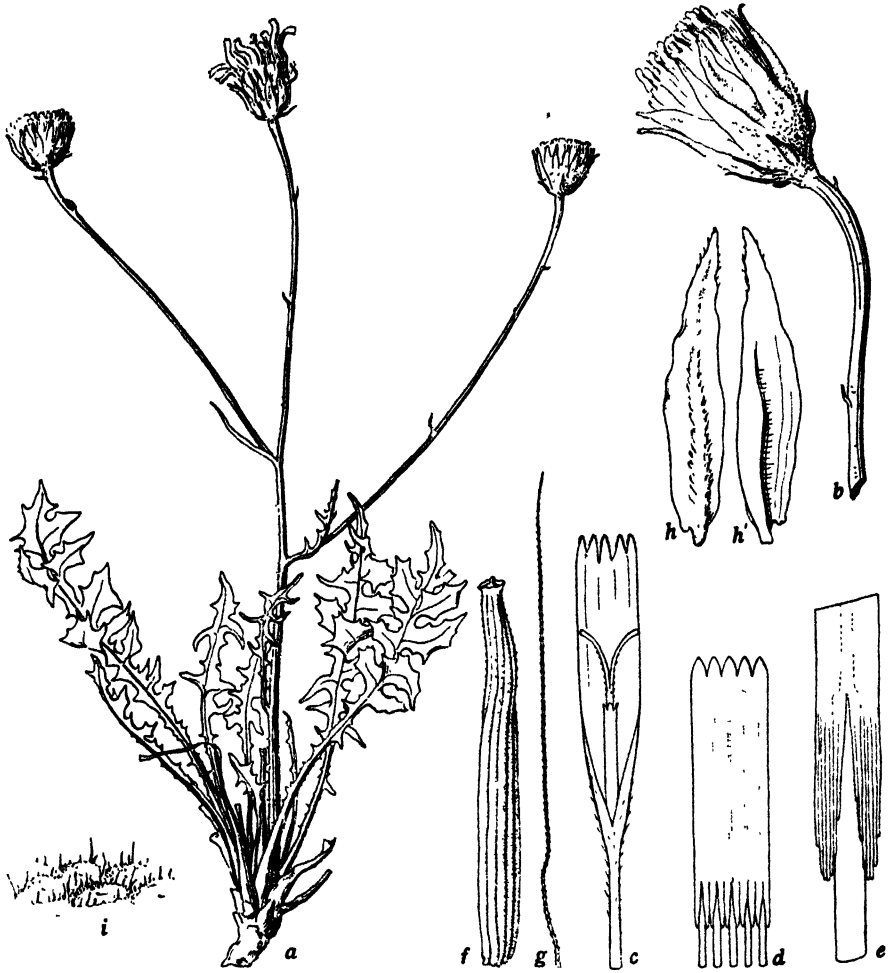


Fig. 120. *Crepis macropus*, a, from type (Bo); b-e, from *Sintenis 512* (US 812084); f-i, *Heldreich 379* and in 1846 (Bo): a, plant, $\times \frac{1}{2}$; b, immature head, $\times 2$; c, floret, $\times 4$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, g, achene and pappus seta, $\times 8$; h, h', inner involucre bract from mature head, outer and inner faces, $\times 4$; i, detail of receptacle, $\times 16$.

Asia Minor, in central, N., and N.W. Turkey, on dry, stony, or rocky hills at elevations from 300 to 1600 m.

Turkey: Lycaonia, west of Koniah, route to Beycheher, *Heldreich 884* in 1845 (Bo, type); Lycaonian Taurus, Kavasch, Haraman dist., 1600 m, *Siehe 554* (B); Galatia, Angora (Ankara), *Wirdman 129* (Bo); Galatia, valley of Fuce Sir, near Ankara, *Krause 3636* (UC); Paphlagonia, Cankri (?), 300 m, *Bornmüller 14337* (US, G); Phrygia, Mt. Bulgaschdag, about 1200 m (acc. to Boissier, Fl. Orient. 3: 837. 1875, this station is 5400 ft., 1636 m), *Balansa 114* (Bo) m.v. 1; Phrygia, Sultandagh, Akseheher (Wilajet Koniah), *Bornmüller 5217* (PA); Lycaonia, Koniah Prov., Ak Chehir, *St.-Leger* in 1907 (NY) m.v. 1; Mysenia, Mt. Ida, north of Edremid and Mt. Szusuzdag, *Sintenis 512* (US).

Minor Variant of C. macropus

1. (*C. macropus* var. *phrygia* Boiss., Fl. Orient. 3: 837. 1875.) Plant 4.5 dm high, the peduncles up to 20 cm long, and the leaves bipinnatifid. Other collections from Phrygia, however, are wholly typical (cf. Bornmüller 5217, cited above), and it seems probable that this variety is based merely on an unusually vigorous plant. *Balansa* 114 (Bo), Mt. Bulgaschdagh, Phrygia.

Relationship

Crepis macropus exhibits closer similarities to its Balkan relatives, especially to *C. albanica* and *C. turcica*, than to those of Asia Minor. In its dissected leaves it resembles *C. incana*; but in its habit, involucre, florets, and achenes it is more like *C. turcica*. It is probably little, if any, more advanced than *C. turcica*.

78. *Crepis oporinoides* Boiss.

Ex DC. Prod. 7: 165. 1838; Boiss., Voy. Bot. Espagne, 2: 388 et 1: t. 117. 1839-1845.
(Fig. 121.)

Perennial, 0.8-4.7 dm high; root vertical or oblique, woody, up to 7 mm wide, 20 cm long, sometimes producing subterranean buds, simple or 2-4-branched at summit; caudex 4-10 mm wide, leafy; caudical leaves 5-23 cm long, 1-3(5) cm wide, oblanceolate, acute to caudate-acuminate, pinnatifid with retrorse triangular or linear close or remote mucronate lateral lobes, sometimes dentate or entire in reduced forms, attenuate into a narrowly winged petiole, with prominent pale midrib, glabrous or \pm pubescent with fine short sometimes glandular hairs; cauline leaves similar or bractlike; stems 1-8, sometimes simple, bracteate, 1-headed, mostly divaricately 1-4-branched beginning near the base, branches remote, elongated, slender, terete, glabrous; peduncles long (up to 25 cm), slender, arcuate, glabrous or tomentulose near head; heads erect, medium, about 30-flowered; involucre cylindric-campanulate, 10-15 mm long, 4-7 mm wide, canescent-tomentulose; outer bracts 8-10, longest $\frac{1}{2}$ as long as inner bracts, linear, with dorsal median nerve becoming thickened; inner bracts 12-14, lanceolate, obtuse, white-ciliate at apex, membranous margined, ventrally appressed-pubescent, dorsally strongly carinate, spongy-thickened at base in fruit, ultimately reflexed; receptacle areolate-fimbriate, fimbriae low, membranous, naked; corolla 14 mm long; ligule 2.2 mm wide; teeth 0.3-0.6 mm long; corolla tube 4 mm long, slender, pubescent with short (up to 0.15 mm) 2-celled acicular hairs; anther tube 4×1 mm; appendages 0.6 mm long, obtuse; filaments 0.6 mm longer; style branches 1.75-2 mm long, yellow; achenes yellowish, 7-9.5 mm long, fusiform, definitely attenuate to the scarcely expanded pappus disk, strongly calloused at the hollow base, 20-30-ribbed, ribs close, narrow, rounded, finely muriculate or spiculate near the apex; pappus pale yellowish, 5-7 mm long, 2-seriate, setae rather fine, coarsest about 35μ (4 cells) wide at base, soft, persistent. Flowering June-Aug.; flowers yellow, reddish-purple on outer face of ligules. Chromosomes, $2n = 8$, but the karyotype unique (see p. 474).

Hieraciodes oporinodes O. Kuntze, Gen. 1: 346. 1891.

S. Spain, in Granada, Almeria, and Jaen, at elevations ranging from 1700 to 3000 m, on calcareous gravels and schists.

This distinct but little known endemic species varies in stature and somewhat in leaf outline according to the altitude. In very low forms, mostly from higher elevations, the divaricate branches or 1-headed stems are procumbent, making a very different looking plant from the tall diffuse forms of lower altitudes. But between the two extremes there are various intergradations, and reduced forms sometimes occur at lower altitudes in dry situations.

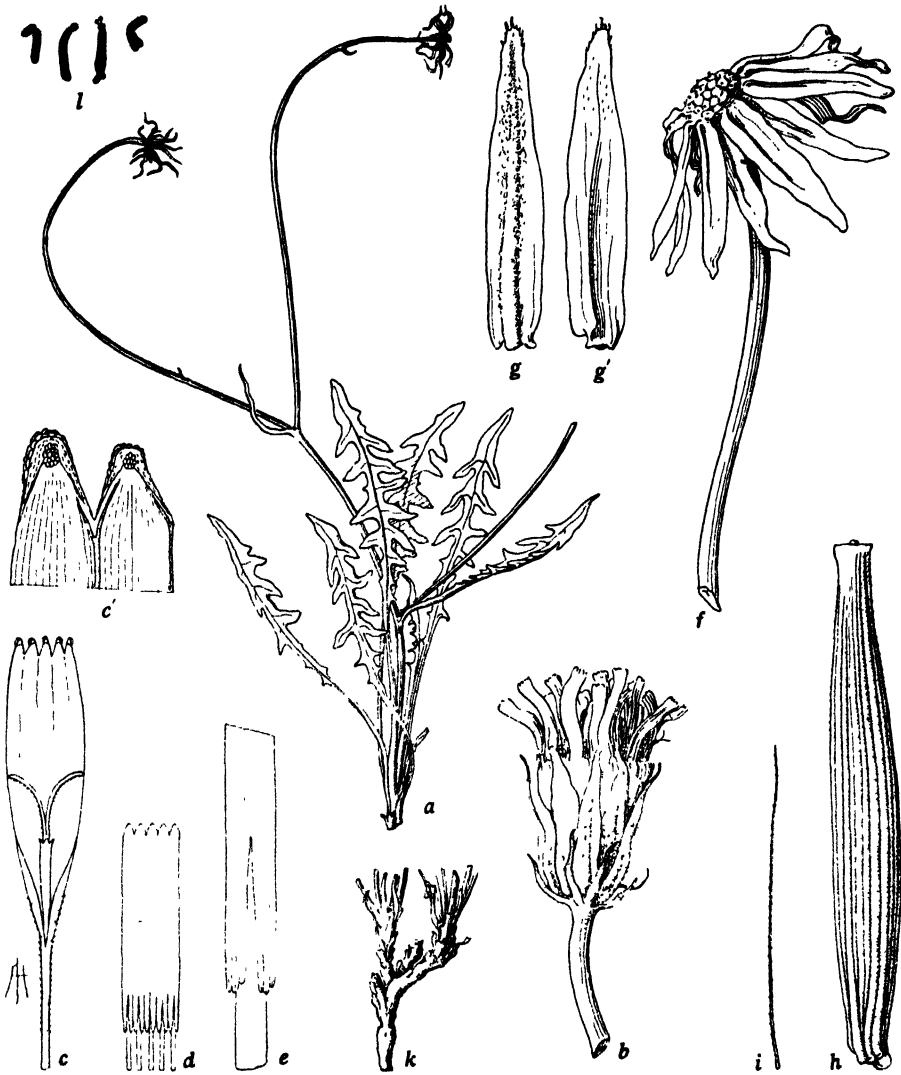


Fig. 121. *Crepis oporinoides*, a, from isotype (CA 68856); b-i, from type (Bo); k, from *Huter, Porta, et Rigo* in 1879 (K); l, from hort. genet. Calif. 3398 (grown from seeds collected by Dr. Cortés Latorre, University of Granada; cf. UC 548432): a, plant, $\times \frac{1}{2}$; b, flowering head, $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule teeth, $\times 50$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, old head and peduncle, $\times 2$; g, g', inner involucre bract from fruiting head, outer and inner faces, $\times 4$; h, i, achene and pappus seta, $\times 8$; k, base of plant, $\times \frac{1}{2}$; l, somatic chromosomes, $n = 4$, $\times 1250$.

Spain: Sierra Nevada, steep slopes and rocks, 2121-2424 m, *Boissier* in 1837 (Bo type, UCF, K, CA); Sierra Nevada, *Boissier* in 1837 (Bo, US) m.v. 1; Granada, Sierra Nevada, Lagunillas, *Munby* in 1848 (K); Sierra Nevada, Barranco de S. Juan, alpine, *Bourgeau* in 1851 (Bo, K, FL); Sierra de Baza, alpine, *Bourgeau* in 1851 (Bo, K, Bur) m.v. 2; Granada, Picacho Veleta, *Winkler* in 1876 (K); *ibid.*, Mt. Dornajo, *Huter, Porta, et Rigo* in 1879 (K, Bur, US) m.v. 1 p. p.; Granada, Mt. Carbario, *Fimines* in 1873 (B); Almeria, Sierra de Maria, *Porta et Rigo* in 1890 (K, Bur); Jaen, Sierra de la Sagra, *Reverchon* in 1900 (Bur, Minn) m.v. 1; Granada, Sierra Nevada, near Laguna de las Yeguas, *Lindberg* 913 (K) m.v. 1; *ibid.*, *Cortés Latorre* in 1935 (UC) m.v. 1; *ibid.*, Peñones de San Francisco, *Cortés Latorre* in 1935 (UC); Sierra Nevada, Puesto de Vacares, 2900 m, *Gros* in 1923 (Bar, UC) m.v. 1; Sierra Nevada, Barranco de Goterón, 2600 m, *Font Quer*

in 1923 (Bar, UC); Sierra Nevada, Horeajo de Freveles, 2400 m, *Gros* in 1923 (Bar, UC); Sierra Nevada, Cerro de Fesoro, near St. Jeronimo, 1800 m, *Font Quer* in 1923 (Bar, UC); Jaen, Sierra de Cazorla, *Reverchon* in 1901 (Ms) m.v. 1; Jaen, N. Sierra Magina, below La Ventana, 1800 m, *Cuatrecasas* in 1926 (Bar, UC) m.v. 2.

Minor Variants of *C. oporinoides*

1. (*C. oporinoides* var. *prostrata* Boiss., Voy. Bot. Espagne, 2: 388. 1839-1845.) Merely a reduced form in which the leaves are often runcinate and obtuse; but similar forms occur with pinnatifid, caudate-acuminate leaves as in at least one plant of the type collection; stems very short, branched at base, with divaricate, procumbent branches, or simple, 1-headed. *Boissier* in 1837 (US) 2878 m, Sierra Nevada; *Huter, Porta, et Rigo* in 1879 (US) 2300-2700 m, Mt. Dornajo, P. Veleta, Sierra Nevada; *Lindberg* 913 (K), 2500 m, Laguna de las Yeguas, Sierra Nevada, Granada, Spain.

2. (*C. oporinoides* var. *floccosa* Bourgeau in herb.) Apparently a local race, characterized by a small rosette of short caudate-acuminate pinnatifid leaves which are sparsely canescent-tomentose and shortly gland-pubescent; stems very short, with procumbent or semierect branches 9-30 cm long. But similar races occur elsewhere, as in the first specimen cited here. *Cuatrecasas* in 1926 (Bar, UC), calcareous gravel, 1800 m, near La Ventana, N. Sierra Magina, Jaen, Spain; *Bourgeau* in 1851 (K), alpine reg., Sierra de Baza, Almeria-Granada, Spain.

Relationship

Crepis oporinoides shows strong general resemblance to *C. Guioliana*, but the two species differ in many details, especially those of the involucre, receptacle, florets, and achenes. *C. oporinoides* has been confused with *C. biennis*, from which it differs strikingly in the woody perennial root, low divaricate habit, few long-peduncled heads and longer many-ribbed achenes. In spite of these differences, however, the two species have certain resemblances, notably the character of leaf dissection, the long narrow outer bracts of the involucre, and the yellow or stramineous fusiform achenes. Although *C. oporinoides* has only 8 chromosomes, it is noteworthy that one of its four pairs is of type E (i.e., a comparatively short chromosome with a median constriction), which is a characteristic feature of all 5-paired species of *Crepis*, but which, as a rule, is absent in the 4-paired species. This fact, and the fact that the satellited D chromosomes in *C. oporinoides* are unusually long, may indicate that it actually originated from a 5-paired species through translocations resulting in the disappearance of one pair of chromosomes. Such an interpretation is consistent with the conception that *C. oporinoides* is related to the 5-paired ancestral stock which gave rise to *C. biennis*.

79. *Crepis dens-leonis* C. Koch

Linnaea, 23 (7): 689. 1850. (Pl. 8. Fig. 122.)

Perennial (or biennial ?), about 3 dm high; root slender, vertical; caudex 0.6-1 cm wide, leafy; caudical leaves 5-7 cm long (or longer), up to 2.5 cm wide, oblanceolate, acute, pinnately parted, with small terminal lobe and several remote pairs of narrow acute lateral lobes, irregularly dentate, lobes and teeth corneous-mucronate, attenuate into short winged petiole much broader at base, glabrescent; cauline leaves similar or acuminate, sessile, uppermost bractlike; stem divaricately 3-4-branched from the base, the branches equally elongated, arcuate, remotely 2-4-furcate or -divaricate, 2-6-headed, glabrescent; peduncles 3-11 cm long, arcuate or divaricate, naked or 1-bracteate, not enlarged near the head; heads erect, medium, estimated about 50-flowered; involucre campanulate, 12-13 mm high, 6-7 mm wide at middle in fruit (estimated), canescent-tomentose; outer bracts about 10, unequal, longest about $\frac{1}{4}$ as long as the inner, linear; inner bracts 12-16, lanceolate, acute, scarious-margined, glabrous on inner face, becoming carinate dorsally and brown spongy-thickened near base in fruit; receptacle alveolate, fimbriellae irregularly dentate; corolla about 17 mm long; ligule about 1.5 mm wide; teeth 0.5 mm

long; corolla tube about 5 mm long; anther tube 4.5×1.25 mm dis.; appendages 0.5 mm long, oblong, acute; filaments about 0.2 mm longer; style branches 2 mm long, 0.1 mm wide, brown in sic.; achenes dark brownish-purple, 5–5.5 mm long, 0.8 mm wide, columnar, laterally compressed, \pm angled, slightly attenuate to both ends, with slightly expanded pale pappus disk, pale-calloused at the hollow base, 18–20-ribbed, ribs nearly equal, except 3–4 irregularly placed stronger ones,

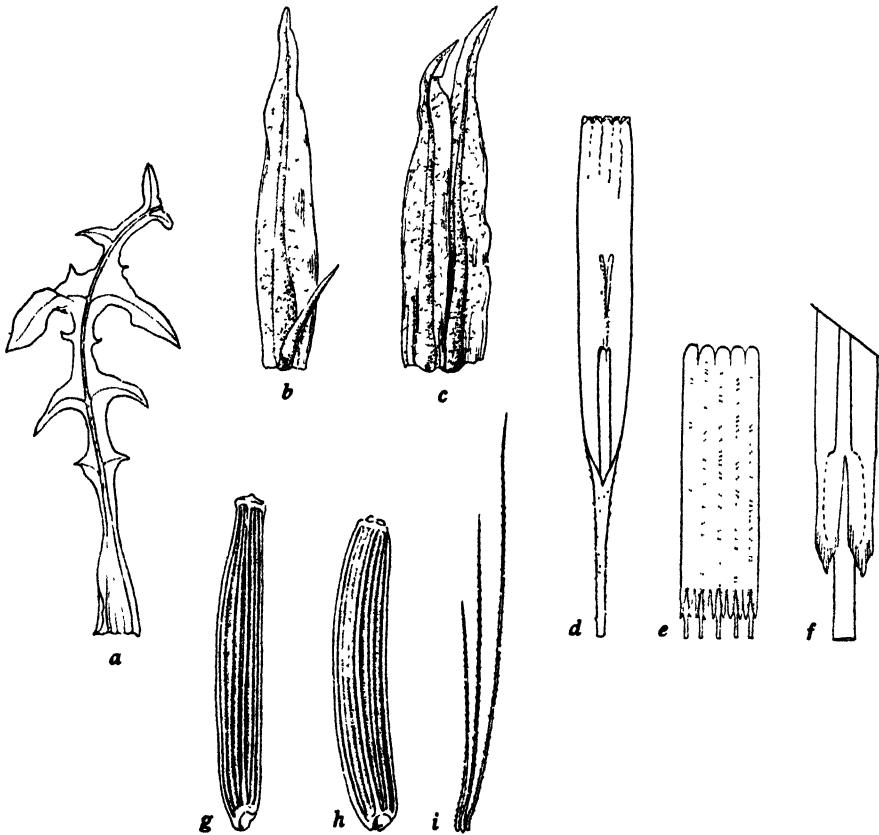


Fig. 122. *Crepis dens-leonis*, from type (B): a, basal part of a caudical leaf, $\times 1$; b, an outer and an inner bract from a flowering head, outer face, $\times 4$; c, 2 inner bracts from a fruiting head, outer face, $\times 4$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 16$; f, detail of appendages, $\times 32$; g–i, 2 achenes and a group of 3 pappus setae, $\times 8$.

rounded, muriculate under lens; pappus white, 6–7 mm long, 3-seriate, setae about equally fine, the coarsest about 30μ (4 cells) wide at base, rather firm but pliable, persistent. Flowers yellow ? (brownish-gray in sic.).

Caucasus. Known only from the original collections of Koch. Only the following statement concerning localities is given with the original description: "Im Gaue Chewi mitten im Kaukasus auf Trachyt und Thonschiefer, c. 5600' hoch," which would be translated literally as follows: *District of Chewi middle Caucasus on trachyte and clayey schist about 1700 m alt.* On the type and duplicate type sheets in Herb. Berol., the locality given is "Caucasus: Chewi" and nothing more. A specimen in herb. Boissier (Genève) has only "Caucasus" on the label; but in herb. Cosson (Paris) there is a specimen with the following: "Caucasus: Kubbak auf Trachyt und Thonschiefer c. 5600'." Although Kubbak is not mentioned in the original publication, it may be assumed that it is a small place in the district of Chewi

in the middle Caucasus. The present author has no information concerning either Kubbak or Chewi. It would seem more likely that they were situated on the N. slope of the range, because localities on the S. slope would probably be designated as Transcaucasia. It should be noted, however, that the town of Chewa is situated in N.E. Turkey, in the E. Pontus reg., just south of the border of Lazistan and about 75 km south of Batum in a mountainous reg. Possibly this is the district where the type and isotypes were collected, whereas Kubbak may be situated in the middle Caucasus.

Monomorphic.

Caucasus: Chewi, *C. Koch* (B, UCf and photograph, type and isotypes); Caucasus, *C. Koch* (Bo); Caucasus, Kubbak, on trachyte and clayey schist, about 1700 m (PC).

Relationship

Although mistaken for an annual by Koch and compared by him with *C. foetida*, and later (in herb. Coss.) confused with that species by Schultz Bipontinus, *Crepis dens-leonis* is almost certainly a perennial (or at least a biennial). This opinion has been confirmed by Dr. J. Mattfeld (in Herb. Berol.). Furthermore, the habit of the plant, its leaves, involucre, and achenes, all indicate that it is related to the other species of this section. It resembles *C. macropus* in many respects, but its achenes are more like those of *C. turcica*.

80. *Crepis Sibthorpiana* Boiss. et Heldr.

Diagn. ser. 1, 11: 56. 1849. (Fig. 123.)

Perennial, 0.3–1.2 dm high; root vertical, elongated, woody, 3–8 mm wide, crowned with a simple or divided caudex 0.5–2.5 cm long, bearing bases of old leaves, leafy at summit; caudical leaves 2–6 cm long, 0.5–1.3 cm wide, oblanceolate, acute or obtuse, runcinately dentate or pinnatifid, terminal segment irregular, lateral segments triangular-acute, canescent-tomentulose or glabrate, attenuate into a short or elongated alate petiole, stramineous or scarious toward the base; cauline leaves few, reduced, the lower similar to the caudical or all bractlike; stem erect, divaricately 3–4-branched, 3–5-headed, the branches mostly short but sometimes relatively long, thus forming a spreading inflorescence, densely tomentose to glabrescent; peduncles 0.2–3 cm long, arcuate, striate or sulcate near head in fruit; heads erect, medium, about 20-flowered; involucre campanulate, 9–10 mm long, 5–7 mm wide at middle in fruit, densely canescent-tomentose; outer bracts 5–8, about $\frac{1}{3}$ as long as the inner in fruit, lanceolate, acute; inner bracts 9–10, oblong-lanceolate, obtuse at apex, membranous-margined, pubescent on inner face with short shining hairs, becoming carinate with a yellow median dorsal keel, spongy-thickened toward base in fruit; receptacle areolate, ciliate with several-celled hairs up to 2 mm long; corolla 9–13 mm long; ligule 1.8–2 mm wide; teeth 0.25–0.5 mm long; corolla tube 2–4 mm long, pubescent with yellow acicular several-celled hairs 0.1–0.8 mm long; anther tube nearly 5×2 mm dis.; appendages 0.7 mm long, lanceolate, acute; filaments only 0.3 mm longer; style branches 1.25–2.25 mm long, 0.1 mm wide, yellow; achenes brown, 4.7–5 mm long, 0.8 mm wide, fusiform, slightly more attenuate near summit, with pale slightly expanded pappus disk, constricted at the yellow-calloused base, 10-ribbed, ribs rather strong, rounded, finely spiculate; pappus white, 5 mm long, 3-seriate, unequal in length and width, the outermost setae shorter and finer, rather stiff but pliable, persistent. Flowering June–Aug.; flowers yellow, ligules purplish-red on outer face.

Hieracium foetidum S. et S., Prod. 2: 134. 1813 et Fl. Graec. t. 799, non Willd.

Crepis divaricata var. *canescens* Boiss. et Heldr., ex Boiss., Diagn. ser. I, 11: 56. 1849.

Hieraciodes Sibthorpium O. Kuntze, Gen. 1: 346. 1891.

Crete, on two of the highest mountain peaks, 1800–2450 m alt.
Monomorphic.

Crete: Sphakia reg., Mt. Stravopodia, about 1800 m, among rocks, *Heldreich* in 1846 (Bo type, K, Bur, UCf); Sphakia reg., mountain summit, 2100 m, *Heldreich* in 1846 (K); central reg. Mt. Ida (Psiloriti), summit, 2450 m, *Baldacci* 234 (Bur, Mo); *ibid.*, *Dörfler* 1099 (Bur, US). Acc. to Halacsy (Consp. Fl. Gr. 2: 216), it was collected on Mt. Stravopodia at Theodori by Raulin, and at Hagion Pneuma by Baldacci. Since it was not found on Mt. Volakia by the author in 1930, it is thus far known only from Mt. Stravopodia and Mt. Psiloriti.

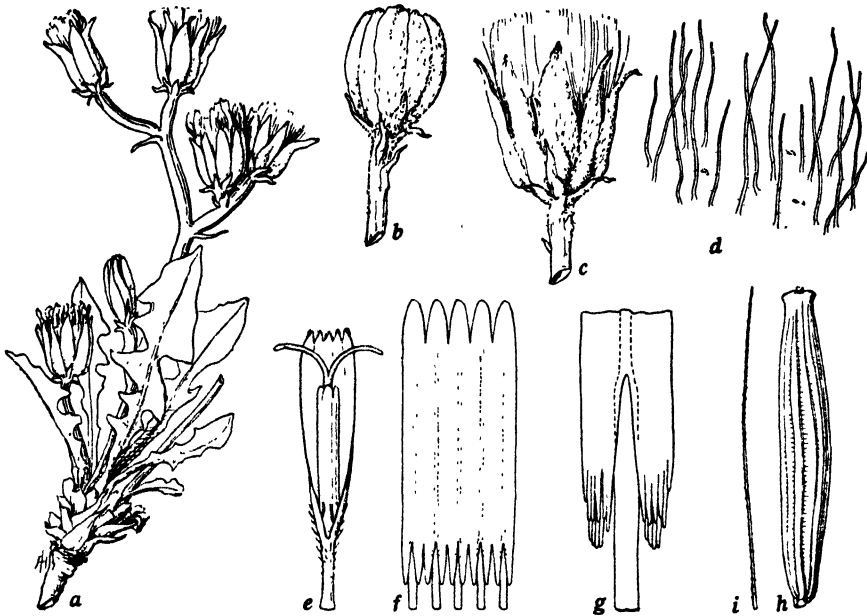


Fig. 123. *Crepis Sibthorpiana*, from *Heldreich* in 1846 (K, Bo): a, plant, $\times 1$; b, young head, $\times 2$; c, mature head, $\times 2$; d, detail of receptacle, $\times 25$; e, floret lacking ovary, $\times 4$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, i, achene and a pappus seta, $\times 8$.

Relationship

Crepis Sibthorpiana, judging from its habit, involucre, and floral characters, is closest, perhaps, to *C. khorassanica*; but since no achenes of *C. khorassanica* have been seen, this opinion must be tentative. From *C. taygetica*, with which it has been confused, *C. Sibthorpiana* differs in many features; yet it does show general resemblance to both *C. taygetica* and *C. incana* in leaves, habit, involucre, and achenes, and to *C. macropus* as well.

81. *Crepis khorassanica* Boiss.

Fl. Orient. 3: 835. 1875. (Fig. 124.)

Perennial, 0.7–1.1 dm high; root vertical, crowned with a simple or divided caudex bearing bases of old leaves and leafy at summit; caudical leaves 3–5 cm long, 0.5–0.7 cm wide, narrowly oblanceolate, gradually attenuate into the alate petiole, retrorsely dentate, \pm glaucous or puberulent, with pale prominent midrib; cauline leaves few, linear, or bractlike; stem or stems shorter than the caudical leaves, 1-furcate and 2-headed, or a little longer and 1-headed; peduncles 5–7 mm long, 1–2-bracteate; heads erect, medium, about 20-flowered; involucre campanu-

late, 10–12 mm long, 5 mm wide at base in anthesis, densely canescent-tomentose; outer bracts few (3–5 ♀), lanceolate, unequal, longest $\frac{1}{2}$ as long as the inner, \pm scabridulous; inner bracts 8–10, lanceolate, acute, dark green, with yellow median line bearing short stout setules, the margins mostly broad, pale and membranous, strigulose on inner face with shining hairs; receptacle ciliate with hairs up to 1 mm long before anthesis; corolla 12–15 mm long (estimated); corolla tube short (2 mm before anthesis), pubescent with yellow acicular several-celled hairs 0.1–0.2 mm long; anther tube 5×1.5 mm dis.; appendages 0.7 mm long, lanceolate, acute; filaments only 0.4 mm longer; style branches before anthesis 1.5 mm long; achenes lacking; pappus yellowish-white, brown at base, about 7 mm long, 2–3-seriate, the setae nearly equal in length and width, rather stiff but pliable. Flowering July (♀); flowers probably yellow and reddish-purple on outer face of ligules, but possibly rose red.

Hieraciodes khorassanicum O. Kuntze, Gen. 1: 346. 1891.

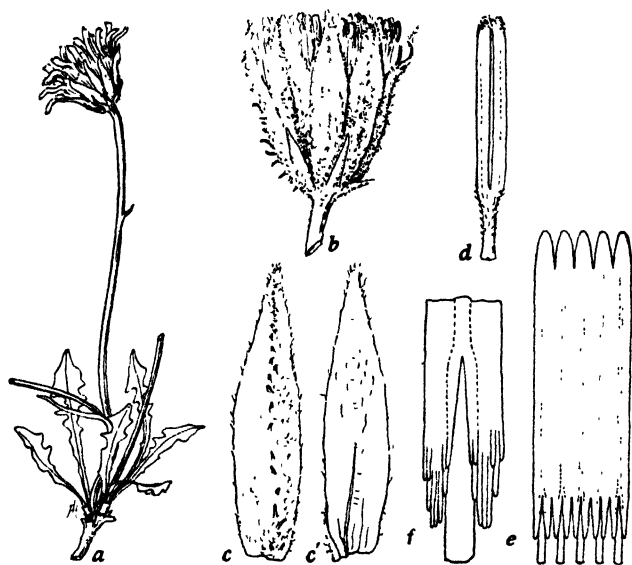


Fig. 124. *Crepis khorassanica*, from type (Bo). a, plant, $\times 1$; b, head, $\times 2$; c, c', inner involucre bract, dorsal and ventral sides, $\times 4$; d, young unopened floret lacking ovary, $\times 4$; e, anther tube, from floret before anthesis, $\times 8$; f, detail of appendages, $\times 32$.

Known only from the type collection of 3 small plants with flowers but no fruits. But the specimen (not seen by me) of Nordmann, referred by Ledebour (R, 827) to *C. incana*, is possibly *C. khorassanica*, although Nordmann's station, "in provinciis transcaucasicis versus fines turcicae," is far to the west of the type locality.

Monomorphic.

N.E. Persia: Khorassan Prov., between Nichapur (Nishapur) and Mesced (Meshed), mountains (Kuh-i-Nishapur), alpine, *Bunge* 267 in 1858 (Bo). Photograph and fragments in Herb. Univ. Calif.

Relationship

This species, on the basis of its low stature, leaves, floral characters, and ciliate receptacle, is probably closest to *C. Sibthorpiana* of Crete. For this reason it is assumed that the inner involucre bracts become thickened as in *C. Sibthorpiana*. Although *C. khorassanica* is similar to *C. Sibthorpiana* in these respects, it is sufficiently different in stem habit, the longer peduncles, and scabridulous involucre,

to warrant retaining it as a species, at least until further collections with mature fruits are available. It is less close to *C. incana* and *C. taygetica* of Greece.

82. *Crepis incana* Sibth. et Smith

Fl. Graec. Prod. 2: 136. 1813. (Fig. 125.)

Perennial, 0.3–1.5 dm high, the leaves, stems, and involucre canescent-tomentose; root woody, elongated, up to 1 cm wide; caudex 1–4 cm long, up to 2 cm wide, simple or divided, dark brown, rugose, leafy above; caudical leaves 3–13 cm long, 1–2 cm wide, oblanceolate, acute, pinnately parted, with lanceolate-entire or triangular-dentate lateral segments, lobes and teeth acute, and corneous-mucronate, attenuate into a short broadly winged petiole, sometimes pubescent with short pale hairs; cauline leaves similar, sessile, amplexicaul, \pm reduced, uppermost bractlike; stems 1–5 or more, robust, divaricately 1–4-branched beginning near base, or simple, 1-headed; peduncles 2–13 cm long, rigid, divaricate, arcuate or erect, bracteate, slightly constricted near the head, sometimes sparsely setose above with short blunt setae or very finely gland-pubescent; heads erect, medium, 30–40-flowered; involucre cylindric-campanulate, 10–12 mm high, about 5 mm wide at middle in fruit, densely canescent-tomentose, shortly setose with a median dorsal row of blunt black setae on outer and inner bracts; outer bracts 8–10, unequal, longest $\frac{1}{2}$ as long as the inner in fruit, lanceolate, acute, dark near the apex; inner bracts about 10, lanceolate, obtuse, glabrous on inner face, becoming carinate and spongy-thickened dorsally at maturity; receptacle alveolate, fimbriae dentate and very shortly ciliate; corolla 14 mm long; ligule 2 mm wide; teeth 0.5 mm long; corolla tube 4.75 mm long, beset with very short papilliform trichomes and sometimes a few fine acicular hairs at base of ligule; anther tube about 4×1.25 mm dis.; appendages 0.6 mm long, oblong, obtuse; filaments 0.4 mm longer; style branches about 2 mm long, slender, yellow; achenes brown, 5–6 mm long, 0.8–1.4 mm wide, fusiform, about equally attenuate to both ends, with slightly expanded pale pappus disk, pale-calloused at the hollow base, 10-ribbed, ribs equal or 3–4 slightly stronger, rounded, smooth or muriculate under lens; pappus white, 8 mm long, 3-seriate, outer series very fine, spreading, middle series intermediate, inner series much coarser, up to 50μ (6 cells) wide at base, soft, deciduous. Flowering June–Aug.; flowers (ligules) magenta-pink, anther tube pink or yellow. Chromosomes, $2n = 16$.

Crepis albida Ch. et B., Nouv. Fl. Pelop. 54. 1838, non All.

Hieraciodes incanum O. Kuntze, Gen. 1, 346. 1891.

Mountains of S. Greece from Phocis and Euboea southward in Attica, Morea, and Peloponnesus, among rocks at middle and subalpine elevations.

Although the type has not been seen by me, the habit drawing (reproduced in our illustration) given by Sibthorp (Fl. Graec. 9: t. 802. 1837) has been compared with the specimens cited below, which have been found quite uniform in their leaves, heads, flowers, and fruits. The specimen of Nordmann from Transcaucasia (not seen by me), which was referred to *C. incana* by Ledebour (R, 827), is more probably *C. khorassanica* (q.v.). Although the latter is a little-known species, it is certainly close to *C. incana*, and Nordmann's plant might be a connecting form; if so, *C. incana*, *C. khorassanica*, and Nordmann's plant may represent different subspecies of a single species. The chromosomes of the latter two should be examined, however, and their comparative morphology and geographic distribution should be investigated, before reaching a conclusion.

Monomorphic.

Greece: Phocis, Mt. Parnassus, Guicciardi 2058 (Bo); *ibid.*, 1200–1500 m, Heldreich 333 (US); Euboea, Mt. Delphi, 1860–1600 m, Heldreich in 1848 (Bo, Bur, K); *ibid.*, 1818 m, Pichler in 1876

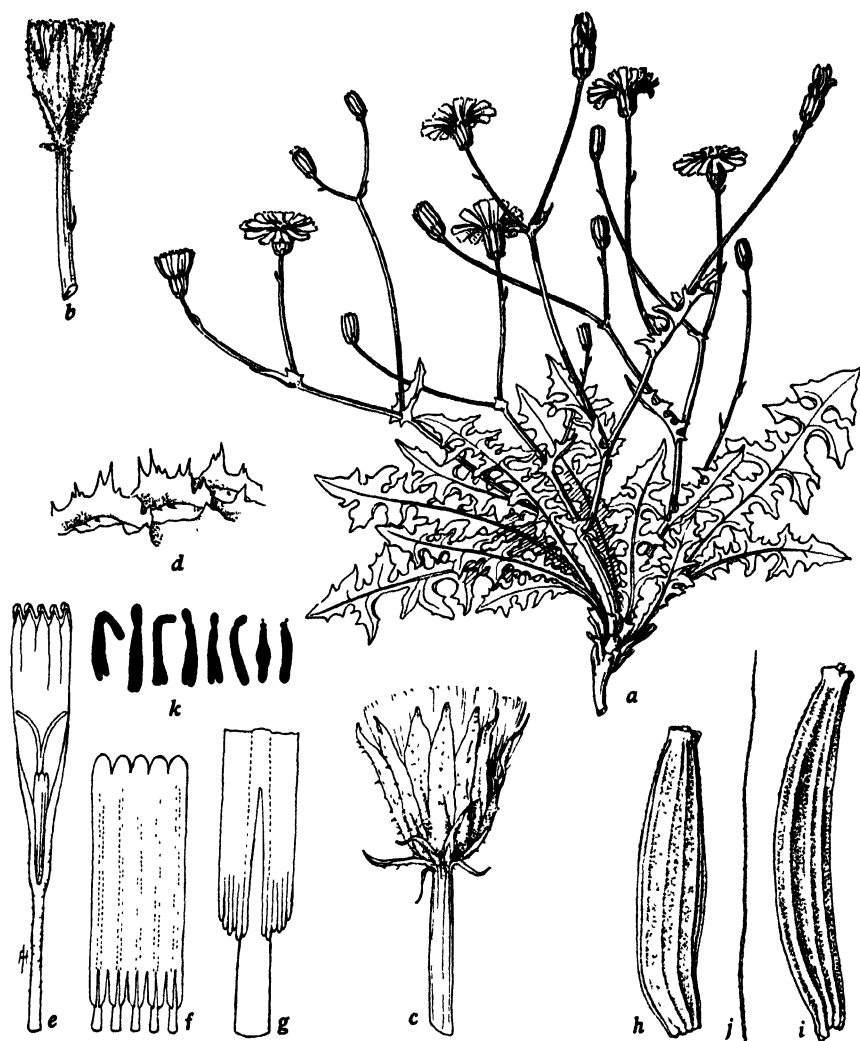


Fig. 125. *Crepis incana*, a, adapted from Sibthorp, Fl. Graec., tab. 802; b-d, from Heldreich in 1848 (K); e-g, from Heldreich 2058 (K); h-j, from Heldreich 2058 (Bo); k, from hort. genet. Calif. 1667 (grown from seeds collected on Mt. Parnes by D. Demades, Hort. Bot. Atheniensis): a, plant, $\times \frac{1}{2}$; b, young head, $\times 2$; c, mature head, $\times 2$; d, detail of receptacle, $\times 25$; e, floret lacking ovary, $\times 4$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h-j, 2 achenes and a pappus seta, $\times 8$; k, somatic chromosomes, $2n = 16$ ($x = 4$), $\times 1250$.

(K, US); Attica, Mt. Parnes, Heldreich 1637 (Bur); *ibid.*, Guiol in 1928, 1929 (UC); Achaia, Mt. Klokos, 1818 m, Orphanides 477 (Bo, Bur, B); Elis, Mt. Olonos, 1818 m, ferruginous rocks, Heldreich in 1848 (Bo).

Relationship

Crepis incana is closest to *C. taygetica* and was at one time confused with it. Although each is a polyploid species, the two are very different in their karyotypes as well as in external morphology, it being necessary only to mention the striking difference in flower color. Because of its adaptation to severe conditions of growth and its attractiveness, this species is well suited to rock garden culture.

83. *Crepis taygetica* Babco.

Univ. Calif. Publ. Bot. 19: 404. 1941. (Fig. 126.)

Perennial, 0.7–1.5, sometimes 3, dm high; root elongated, slender, woody, branching above, forming several caudices; caudex swollen, leafy, 1–5-stemmed; caudical leaves numerous, 5–10 cm long and up to 1.7 cm wide, oblanceolate, acute, runcinately dentate or pinnately lobed, lateral segments triangular or lanceolate, acute, gradually attenuate into the narrowly winged petiole with broader clasping base, midrib pale, becoming thickened and indurate near base, pubescent with pale glandless hairs, canescent-tomentulose on both sides; cauline leaves mostly small, linear, entire; stems numerous, terete, rigid, divaricately much branched from base upward, forming an intricately branched many-headed mound; peduncles 1–10 cm long, arcuate, terete, glabrescent or tomentulose, 1–4-bracteate, becoming thickened and rigid after anthesis; heads erect, medium, about 15-flowered; involucre cylindrical, 10–12 mm high, 4 mm wide near base in fruiting heads, canescent-tomentulose; outer bracts 5 or 6 with 3 or 4 subtending ones, unequal, longest $\frac{1}{3}$ as long as inner ones, linear, obtuse, white-ciliate at apex; inner bracts 8, lanceolate, obtuse, white-ciliate at apex, membranous-margined, becoming dorsally keeled and conspicuously spongy-thickened, sometimes with a median dorsal row of short black setae, glabrous within; receptacle alveolate-fimbriate, fimbriae 0.5 mm high, shortly ciliate; corolla in marginal florets 18 mm long; ligule 2.5 mm wide; ligule teeth 0.75 mm long; corolla tube 6 mm long, thickly beset with minute white 2-celled hairs; anther tube 5.3×1.5 mm dis.; appendages 1 mm long, oblong, acute, notably fringed at tip; filaments only 0.2 mm longer; style branches yellow, 2.25 mm long; achenes chestnut brown, 5.5 mm long, 1 mm wide, fusiform, nearly equally attenuate to both ends, pappus disk white, scarcely expanded, base hollow, yellow-calloused, ribs 10, rounded, smooth or finely spiculate near the apex; pappus white, 6 mm long, 3-seriate, fine, soft, deciduous. Flowering June–Aug.; flowers yellow, with purplish-red stripe on outer face of ligule. Chromosomes, $2n =$ about 40.

Crepis divaricata Boiss. et. Heldr., Diag. Pl. Or. Nov. ser. 1, 7: 13. 1846; Boiss., Fl. Or., 3: 836. 1875, non *Crepis divaricata* (Lowe) F. Sch.

Hieraciodes Heldreichianum O. Kuntze, Gen. 1: 345. 1891, nomen nudum.

Monomorphic.

Greece: Peloponnesus; Laconia, Taygetus (Pentadaktylon) Mts., Mt. St. Elias, among rocks along trail from above timber line to a point called "Porta," which is about 2300 m alt. Known to me only from this locality, which, acc. to Heldreich, is called Kakochioni, and which is just north of the conspicuous landmark known as Megala Zonaria. *Heldreich* 401 in 1844 (Bo type, K, UCf, Fl); *Heldreich* 1453 in 1897 (K); *Pichler* in 1876 (K, Bo, Bur); *Maire et Petitmengin* 973 (Ms, Bur); *Babcock* 331 (UC). The report of Markgraf (Fedde Rep. Sp. Nov. Veg. 30: 854. 1931) that this species occurs in Macedonia has not been verified by me.

Relationship

Crepis taygetica has been confused with *C. Sibthorpiana* of Crete, the chromosomes of which have not yet been studied; and it is considered by some as the same species (cf. Markgraf, 853). But the two are very distinct in floral characters as well as in their achenes and notably in the surface of the receptacle, which is alveolate in *taygetica* and plain but long-ciliate in *Sibthorpiana* (cf. figs. 123, 126). The little-known *C. khorassanica* also differs from *C. taygetica* in floral characters and in having the involucre bracts pubescent within. This species is probably closest to *C. incana*, which is very distinct. There is evidence of phylogenetic connection of these species with *C. macropus* and *C. turcica*, particularly the similar involucre,

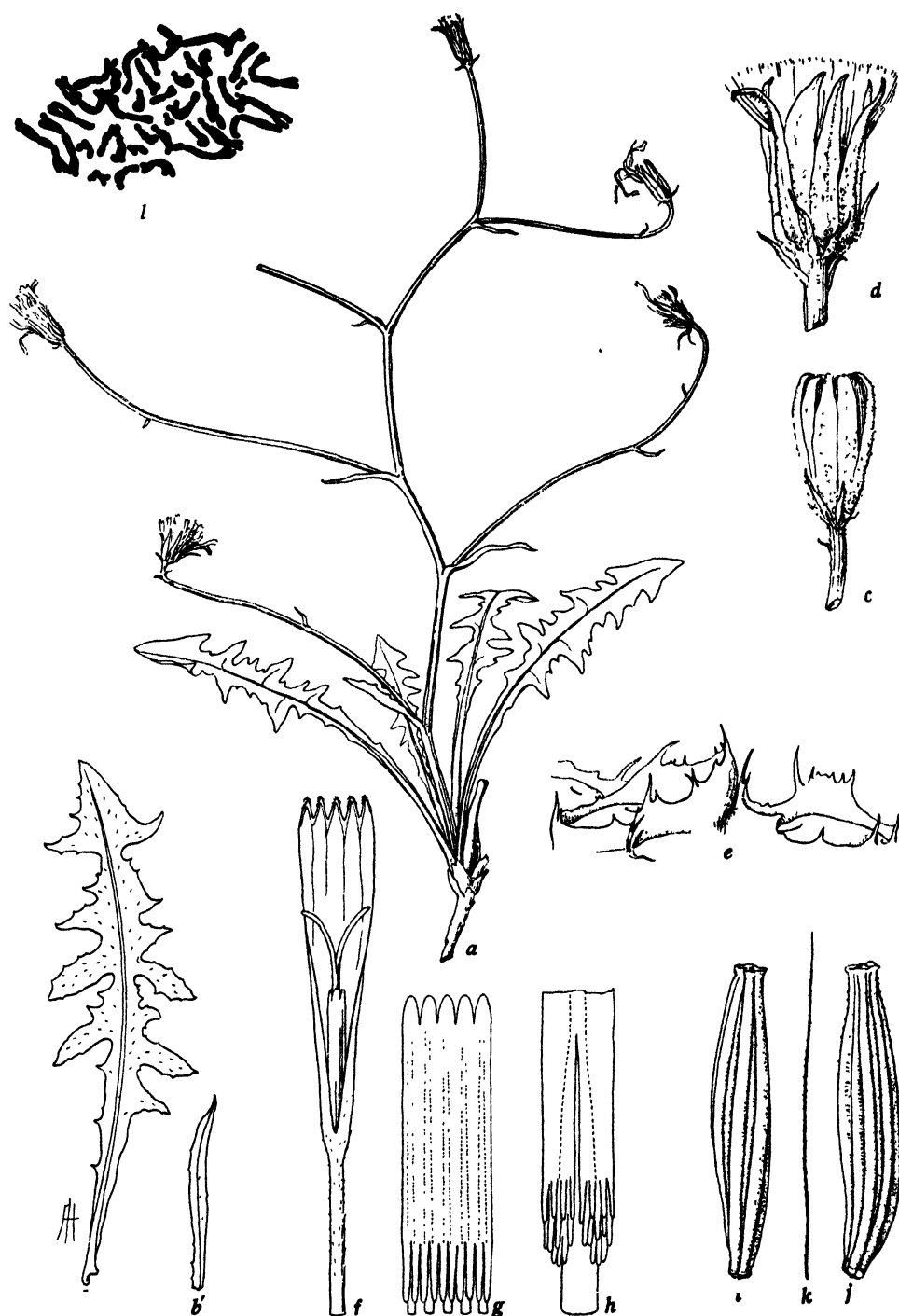


Fig. 126. *Crepis taygetica*, a-k, from Heldreich in 1897 (K) and Heldreich in 1844 (K, Fl); l, from hort. genet. Calif. 30.2893, plants grown from roots collected at loc. class., Babcock 531 (UC 429384): a, plant, $\times \frac{1}{2}$; b, b', caudical and cauline leaves, $\times 1$; c, d, young and old heads, $\times 2$; e, detail of receptacle, $\times 25$; f, floret lacking ovary, $\times 4$; g, anther tube, $\times 8$; h, detail of appendages, $\times 32$; i-k, 2 achenes and a pappus seta, $\times 8$; l, somatic chromosomes, $2n = \text{about } 40$, $\times 1250$.

florets, and fruits, as well as the habit and leaves. The chromosomes of *C. taygetica* are very different from those of *C. incana*, which is certainly a tetraploid with $x=4$. In the only available plate that is countable (cf. fig. 126, l), *C. taygetica* shows 41 chromosomes, and there are clearly 5 distinct types; yet there are more than eight of certain types in this plate, and less than 8 of the shortest chromosome. Thus, *C. taygetica* appears to be a modified octoploid with $x=5$. Since *C. taygetica* is a higher polyploid than *C. incana*, it may be more recent, although it probably originated from a 5-paired ancestor or ancestors.

By means of the long woody root, plants of this species are able to maintain themselves for a considerable number of years in difficult situations among broken rocks on steep mountain sides at alpine elevations. The plants are easily grown out-of-doors at sea level and will live for several years in large pots. This species should prove very satisfactory in an alpine rockery.

SUBSECTION F. STRICTAE

84. *Crepis turcomanica* H. Krasch.

Acta Inst. Bot. Acad. Sci. U. S. S. R. ser. I. 1: 181. 1933. (Fig. 127.)

Perennial, 3–4 dm high; root elongated, straight or curved; caudex slender and simple or thicker and \pm divided at crown, woody, brown; caudical leaves few, disappearing; lower cauline leaves up to 15 cm long, 1 cm wide, oblanceolate, acute or acuminate, remotely denticulate or dentate, teeth narrow, acuminate, gland-puberulent, especially beneath, with short pale hairs and small brown glands; middle cauline leaves lanceolate or linear, acuminate, sessile, semiamplexicaul or amplexicaul, acutely auriculate, finely puberulent; uppermost leaves linear, bract-like; stem simple, 3-headed or stems several, branched above, few-headed, slender, terete, gland-puberulent below; branches pedunculate or 2-headed, elongated, rather strictly erect or somewhat arcuate, 1–3-bracteate, somewhat thickened, sulcate and canescent-tomentulose near head, obscurely hispidulous below, gland-pubescent or tomentulose at bifurcations; heads erect, large, many-flowered; involucre campanulate, 13–17 mm high, about 8 mm wide near middle in fruiting heads, canescent-tomentulose; outer bracts 5–6, very unequal, $\frac{1}{2}$ – $\frac{3}{4}$ as long as inner bracts, linear, acuminate, dark green; inner bracts about 12, lanceolate, obtuse, the median region dark green, pubescent with short glandless or glandular hairs, the marginal region yellow, scarious, glabrous on inner face, becoming rounded-carinate, spongy-thickened at base, and indurate in fruit; receptacle alveolate, alveoles 0.5–0.75 mm wide, fimbriae 0.5 mm high, rather fleshy, densely ciliate with yellowish crinkled hairs 1–2 mm long; corolla 21 mm long; ligule 2.5–3 mm wide; teeth 0.3–1 mm long; corolla tube 6 mm long, pubescent, like base of ligule, with stout 2–3-celled acicular hairs 0.05–1 mm long; anther tube 6.5×1.5 mm dis.; appendages 0.8–1 mm long, oblong, obtuse; filaments 0.6 mm longer; style branches 3.5 mm long, 0.2 mm wide, obtuse, yellow; achenes tawny, 6–7.5 mm long, 1 mm wide, fusiform, attenuate upward to the thickened expanded pappus disk, slightly constricted at the strongly calloused truncate base, about 15-ribbed, ribs narrow, rounded, finely spiculate, alternate ribs a little stronger, marginal achenes shortly white-ciliate at summit just below pappus disk, cilia early deciduous or sometimes absent; pappus white, about 7 mm long, 2-seriate, rather fine, soft, deciduous. Flowering June–Aug.; flowers yellow.

S.W. Turkestan, Transcaspian Prov., Turcomania (= Tekke-Turkmenia or Turkmenistania), N. slope of Achal Tekke Mts., in the dist. south of Aschabad. Known definitely only from the dist. mentioned; but probably also occurs in N.E. Iran; also see m.v. 1.

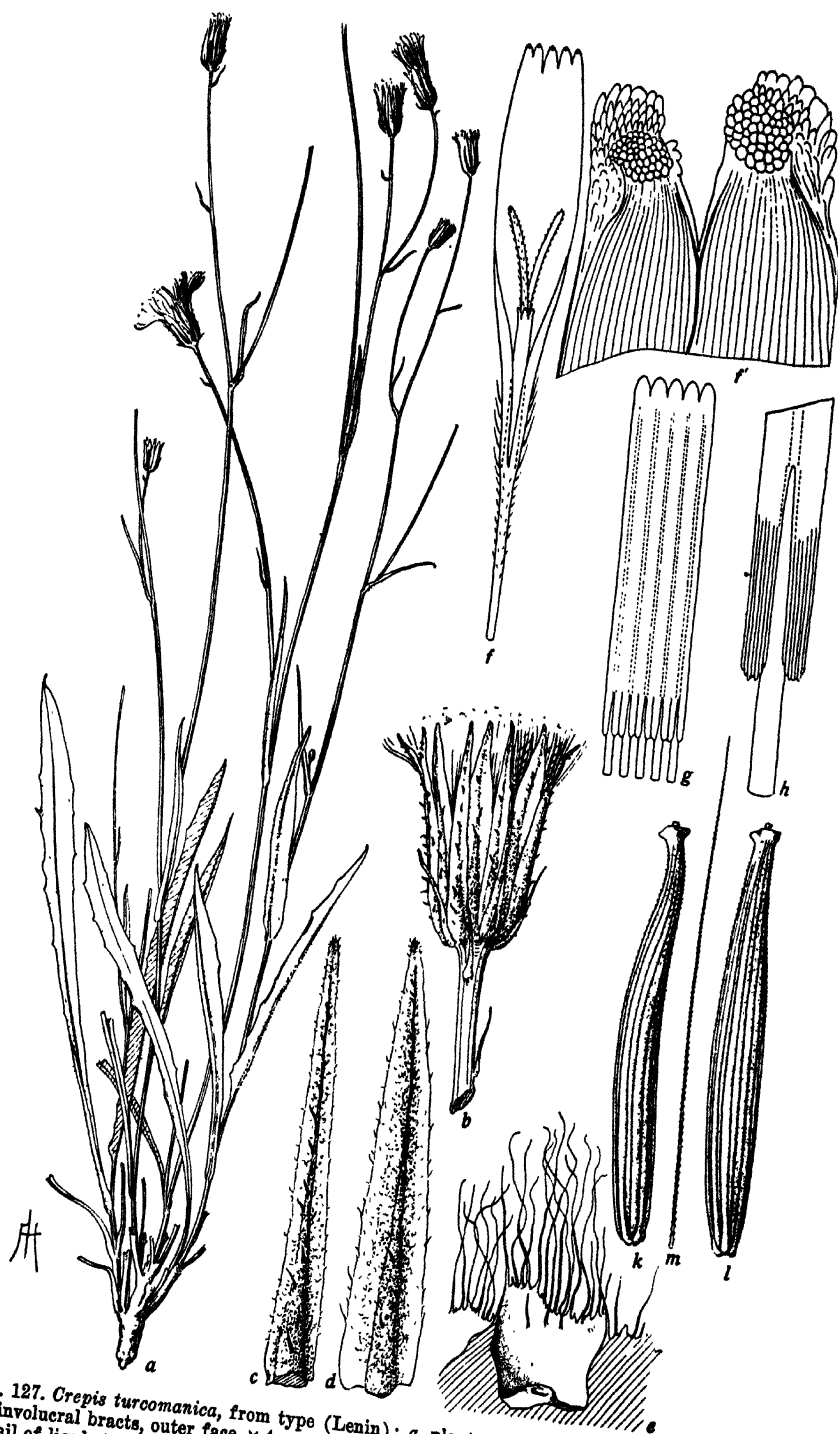


Fig. 127. *Crepis turcomanica*, from type (Lenin): *a*, plant, $\times \frac{1}{2}$; *b*, fruiting head, $\times 2$; *c*, *d*, inner involucre bracts, outer face, $\times 4$; *e*, detail of receptacle, $\times 25$; *f*, detail of ligule teeth, $\times 50$; *g*, anther tube, $\times 8$; *h*, detail of appendages, $\times 32$; *k-m*, 2 achenes and a pappus seta, $\times 8$.

Turcomania: vicinity of Aschabad, Mt. Kopet-dagh, Karanki Canyon or Valley, near Ludus, 1500 m, *Litwinow 1410* (Lenin, UCh) type; mts. near Cheirabad, *Litwinow 1564* (Lenin, CA). Other stations given by Krascheninnikov (*loc. cit.*) are: between Firusa (= Firuze ?) and Ozaisendag; and near the village of Obrucezevo.

Minor Variant of C. turcomanica

1. (*C. sonchifolia* var., C. Winkl., in herb.) Plant low, from a thick pluricipitate caudex; caudical and lower cauline leaves numerous, lance-linear; branches few-headed; fruits lacking. More detailed study may show this plant to be some other species, even though it resembles *C. turcomanica* more than *C. sonchifolia* in caudex and leaves. Accordingly, it is cited here provisionally. *A. Regel* (Fl), north of Kul-i-Kalan, 3030–3333 m, Sarawschan (Sarafschan ?), E. Turkestan.

Relationship

Crepis turcomanica is closest to *C. Guioliana* of the W. Balkans, from which it is easily distinguished by the longer involucre with very long outer bracts, the inner bracts glabrous within, the much longer florets, style branches, anther tubes and appendages, and the strongly ciliate receptacle. It is less close to *C. sonchifolia* of subsection C.

85. *Crepis Guioliana* sp. nov.

(Fig. 128.)

Herba perennis 4–4.5 dm alta; radix tenua lignea; caudex brevis; folia caudicalia numerosa interdum 15 cm longa 2 cm lata oblanceolata acuta vel acuminata sinuata dentata glanduloso-pubescentia, pilis brevissimis, caulina similia vel linearia; caules erecti ramosi, ramis elongatis pedunculatis 10–35 cm longis; capitula mediocria circa 40-flora; involucre cylindricum 10–13 mm longum 7–9 mm latum tomentosum, squamis exterioribus 10–12 inaequalibus lanceolatis acuminatis, interioribus 12–16 lanceolatis acutis viridis ventrale pubescentibus in maturitate spongioso-incrassatis; receptaculum planum areolatum, fimbriis breve ciliatis; corolla circa 13 mm longa, ligula 8.5 mm longa interdum 3 mm lata, tubo pubescenti; antherae circa 5 mm longae; rami styli 2.5 mm longi flavi; achaenia fulva 7 mm longa fusiformia ad apicem constricta 16–20-costata; pappus albus 5–7 mm longus copiosus persistens.

Perennial. 4–4.5 dm high; root woody, slender; caudex short, divided at crown, covered with brown bases of old petioles; caudical leaves numerous, ascending, up to 15 cm long, 2 cm wide, oblanceolate, tapering into a slender petiole equal to or longer than the blade with broad clasping base, acute or acuminate, pinnately sinuate-dentate, teeth acuminate and mucronate, sparsely canescent-tomentulose, minutely gland-pubescent on both sides, glands brown; lower cauline leaves similar, upper cauline leaves linear, entire, short petioled or sessile; stems 2 from each division of the caudex, erect, branched below, branches 2–5, long, pedunculate; peduncles 10–35 cm long, naked or with 1 small bract about midway and sometimes with 1 or 2 minute bracts below head, slightly swollen at base of head, finely striate; heads erect, medium, about 40-flowered; involucre cylindric, 10–13 mm high, 7–9 mm wide, canescent-tomentose; outer bracts 10–12, unequal, the longest $\frac{1}{2}$ – $\frac{2}{3}$ as long as inner bracts, lanceolate, acuminate; inner bracts 12–16, lanceolate, acute, dark green, becoming dorsally spongy-thickened near base, ventrally pubescent with coarse shining hairs; receptacle flat, areolate-fimbriate, fimbriellae membranous and shortly ciliate; corolla about 13 mm long; ligule up to 3 mm wide; teeth 0.3–0.4 mm long; corolla tube 4.5 mm long, sparsely beset with papilliform hairs 0.1 mm long; anther tube about 5.2×1.3 mm dis.; appendages 0.45 mm long, acute, united; filaments short, stout; style branches 2.5 mm long, 0.1 mm wide, attenuate, yellow; achenes tawny, 7 mm long, fusiform, definitely attenuate near the constricted apex, with delicate expanded pappus disk, constricted at base, 16–20-ribbed, ribs narrow

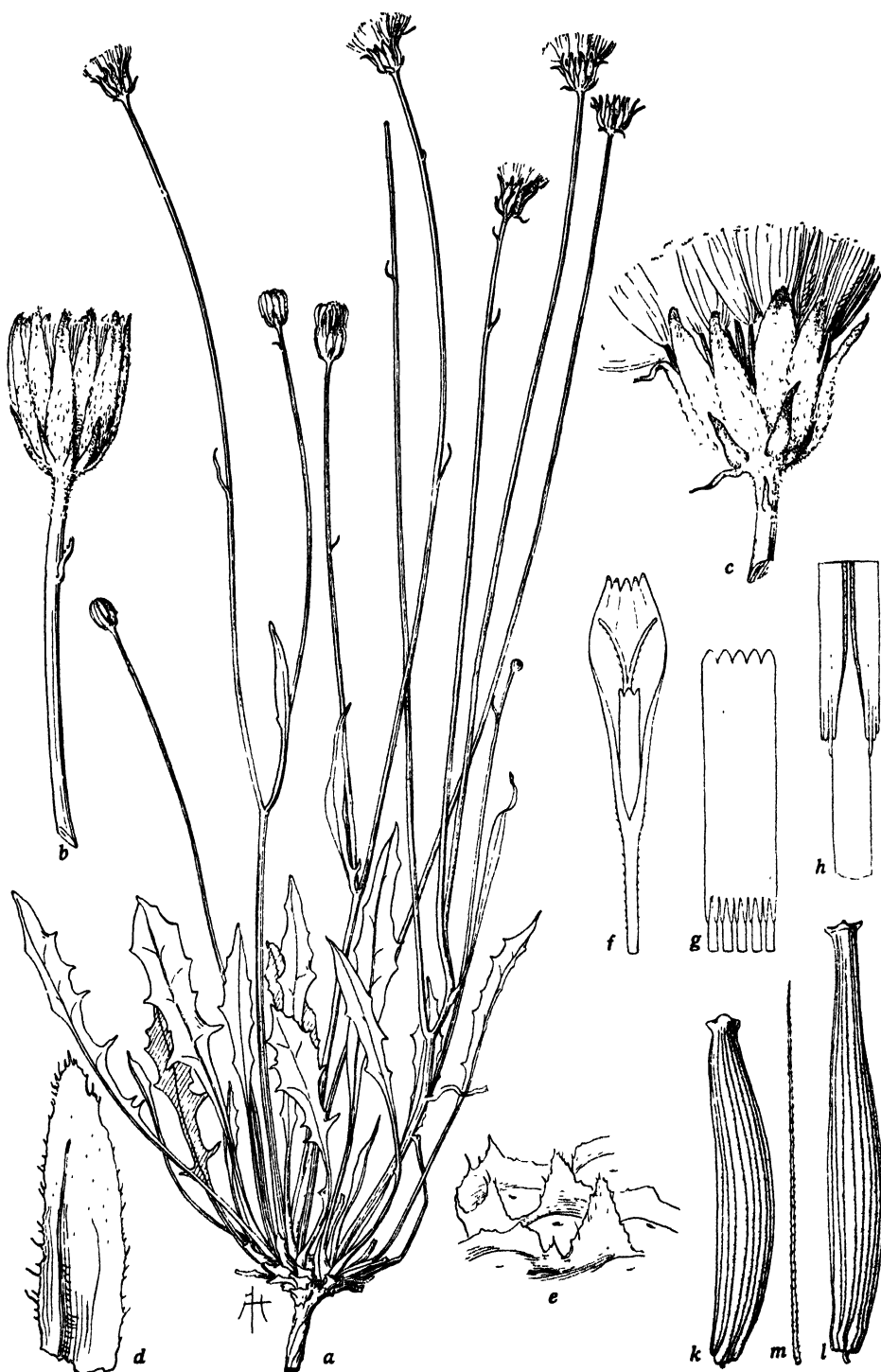


Fig. 128. *Crepis Gujoliana*, from type (UC 476304): a, plant, $\times \frac{1}{2}$; b, young flower head, $\times 2$; c, mature head, $\times 2$; d, inner involucre bract, ventral face, $\times 4$; e, detail of receptacle, $\times 25$; f, floret lacking ovary, $\times 4$; g, anther tube, $\times 8$; h, detail of appendages, $\times 32$; k-m, 2 achenes and a pappus seta, $\times 8$.

or alternate ones wider, somewhat thickened at the base; pappus white, unequal, 5–7 mm long, copious, fine, persistent, coming away in clumps. Flowering July; flowers yellow.

Known only from the type specimen. Named for my friend, F. G. Guiol, who collected it July 29, 1931.

Monomorphic.

Greece: Epirus, Mt. Smolika, above Sumarina, *Guiol 1952* (UC 476304) type.

Relationship

Crepis Guioliana, although so similar in habit and leaves as to be easily mistaken for the little-known species *Crepis athoa* Boiss., is very distinct from it in its larger heads, broader lanceolate involucre bracts with the inner bracts ventrally pubescent, in its wider ligules, larger paler achenes, longer and coarser pappus, and much longer style branches. Also, in *C. athoa* the tawny wool between the bases of the old leaves and at lower bifurcations of the stems is sometimes conspicuous, whereas in the type of *C. Guioliana* this wool is absent or at most very minute. The two species, however, are closely related, and they are also near, but less close, to *C. crocifolia*. *Crepis Guioliana* also exhibits general resemblance to *C. turcomanica*, but differs from it in many details.

86. *Crepis crocifolia* Boiss. et Heldr.

Diag. Pl. Or. Nov. ser. 1, 7: 14. 1846. (Fig. 129.)

Perennial, up to 2.6 dm high, root vertical, very slender, 0.5–3 mm wide below the much thicker caudex; caudex 0.3–2 cm wide including the numerous brown bases of old leaves, simple or divided, 1–4-stemmed; caudical leaves numerous, caespitose, 4–8 cm long, 2–4 mm wide, linear or the lowest narrowly oblanceolate, acute or somewhat obtuse, entire, gradually narrowed into the winged petiole, with broader scarious or purplish base, grayish-glaucous; lowest cauline leaves similar, up to 6 cm long, 1–2 mm wide, the others remote, gradually reduced or bractlike; stems stiffly erect or sinuate, slender, terete, striate, glabrous, bearing a terminal flowering or fruiting head and developing a very slender 1–2-headed branch in the axil of each cauline leaf; peduncles 3–13 cm long, definitely thickened upward but constricted at base of head, glabrous; heads erect, small, 11–14-flowered; involucre campanulate, about 10 mm high, brownish-black in sic., sparsely canescent-tomentulose; outer bracts about 8, unequal, longest $\frac{1}{3}$ as long as the inner, lanceolate, acute; inner bracts 9–10, lanceolate, acute, glabrous on inner face, becoming weakly carinate and spongy-thickened at base in fruit; receptacle glabrous; corolla about 14 mm long; ligule about 2.5 mm wide; teeth about 0.6 mm long; corolla tube 4 mm long, glabrous; anther tube 5×1.7 mm dis.; appendages 0.6 mm long, lanceolate; filaments 0.6 mm longer; style branches 2 mm long, 0.1 mm wide, yellow; achenes stramineous, 5–5.5 mm long, 0.6–0.7 mm wide, slightly curved or straight, subterete, more strongly attenuate upward, 0.3–0.4 mm wide below the expanded pappus disk, slightly narrowed at the thin-calloused hollow base, about 20-striate, striae weak, smooth; pappus pale yellowish, about 5 mm long, 2-seriate, setae unequal in width, coarsest about 50μ , finest about 16μ at base, outermost setae coarser, rather rigid and brittle, persistent. Flowering July–Aug.; flowers yellow.

Hieraciodes crocifolium O. Kuntze, Gen. 1: 345. 1891.

Greece, Morea (Peloponnesus), in the Pentadaktylon Mts. (Oros Taygetos or Taygetus), between Messenia and Laconia, at a high altitude, among rocks.

Although there is a confusion of place names on the labels with the original col-

lections, de Heldreich himself removed all doubt concerning the exact location of at least part of the type collection by his statement in herb. Graec. Norm. n. 1452, "Mt. Taygetus, reg. alp., Megala Zonaria et Choupata (loc. class, et unico ?)." Megala Zonaria is a conspicuous landmark just below Hagios Elias, the highest point in the range, the altitude of which is about 2400 m. Whether Choupata (Kou-

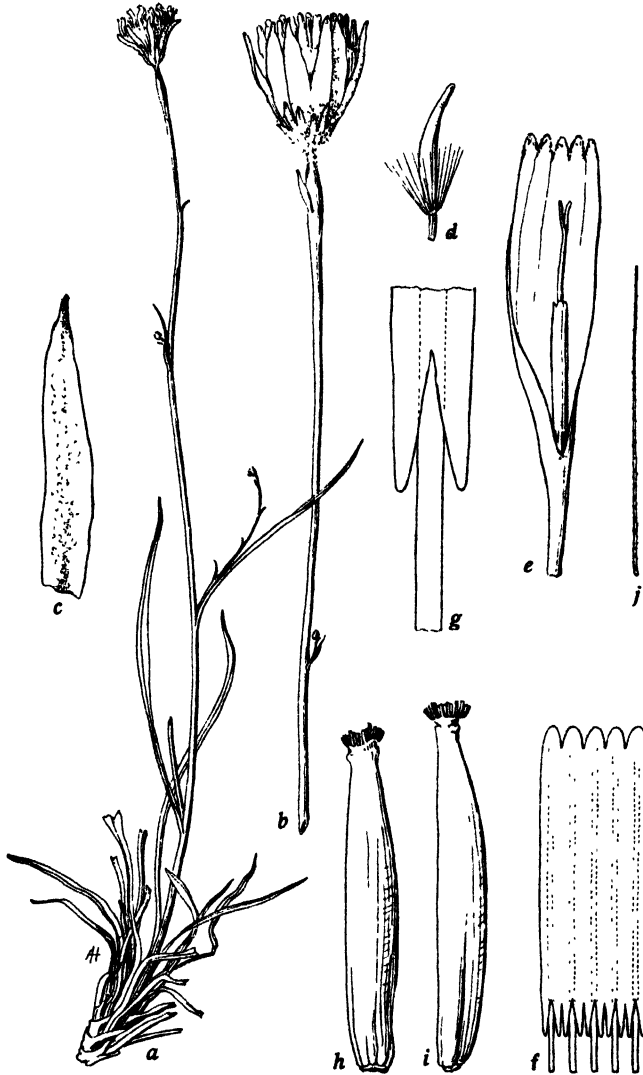


Fig. 129. *Crepis crocifolia*, from Heldreich in 1844, including type (Bo): a, plant, $\times \frac{1}{2}$; b, head and peduncle, $\times 2$; c, inner involucral bract, outer face, $\times 4$; d, young floret, $\times 2$; e, floret lacking ovary, $\times 4$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, i, achenes, with pappus setae broken off, $\times 8$; j, a pappus seta, $\times 8$.

pata) is closely associated with Hagios Elias or is situated at some distance away is uncertain. Another source of confusion in localities is the appearance of "Hagios Paraskevi" on some of the labels with de Heldreich's original collections. Two places of that name are given in Stieler's Atlas, one in Lesbos (Midillü I.) and the other in Kassandra. To my knowledge there is no such place in the Pentadaktylon Mts., and it is noteworthy that de Heldreich omitted it in his later distribution of speci-

mens of this species. The present writer is convinced that the plant is rare in the vicinity of Megala Zonaria, because his search for it there in 1930 was without result.

Monomorphic.

Greece: Mt. Taygetos, among rocks, lower part of central high reg., Hagios Paraskevi (note that on Hagios Elias the "lower part of central high reg." would be Megala Zonaria), *Heldreich* 373, July 30, 1844 (Bo) type, photograph and fragments (UC); Mt. Taygetos, among rocks, high region at Choupata, *Heldreich* 373, July 24, 1844 (Bo); Taygetus, high region, Hagios Paraskevi and a place called Koupata, *Heldreich* in Aug., 1844 (Bo, Fl); Mt. Taygetus, alpine reg., Megala Zonaria and Choupata (loc. class. et unico ?), *Heldreich* in herb. Graec. Norm. n. 1452 (Bur); Morea, Taygetos Mts., *Pichler* in 1876 (Bur).

Relationship

Crepis crocifolia is very distinct from all the other species in this subsection in its extremely narrow leaves and faintly striate achenes; yet it is very similar to them in habit, and the achenes are similar, both in shape and the numerous striae, to the achenes of the three preceding species. In the feature last mentioned, as well as in size of florets and achenes, it is a less-advanced species than *C. athoa*.

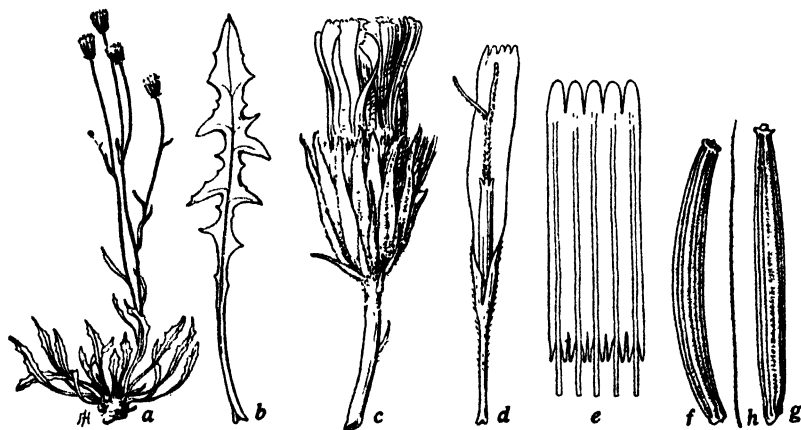


Fig. 130. *Crepis athoa*, a, f-h, from type (Bo); b, from topotype (herb. Chabert, Fl); c-e, from topotype (Bo): a, plant $\times \frac{1}{6}$; b, leaf, $\times \frac{1}{2}$; c, head, $\times 2$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f-h, outer and inner achenes and pappus seta, $\times 8$.

87. *Crepis athoa* Boiss.

Diag. Pl. Or. Nov. ser. 1, 11: 57. 1849. (Fig. 130.)

Perennial, 1.5–3.5 dm high; root slender or stout, woody and branched at summit; caudex 1–3 cm wide, covered with conspicuous brown bases of old leaves, with sometimes inconspicuous tawny wool at bases of leaves and nodes; caudical leaves numerous, ascending, 5–15 cm long, 0.5–3 cm wide, oblanceolate, acute, dentate to runcinate-pinnatifid, with triangular acute teeth or lobes, glabrescent or tomentulose at base; cauline leaves few, linear, acute, or acuminate, entire; stem or stems erect, slender, terete, striate, glabrous except at base and bifurcations, remotely cymosely branched from middle or near base, branches elongated, pedunculate; peduncles slender, glabrous, 1–3-bracteate, becoming somewhat thickened near head, sometimes stramineous; heads erect, medium, about 40-flowered; involucre campanulate, 9–10 mm long, 5–7 mm wide at middle in fruit, canescent tomentulose; outer bracts 10–12, unequal, longest $\frac{1}{2}$ as long as inner, subulate, black toward apex; inner bracts 12–14, lanceolate, acute, ciliate at tip, with black median dorsal stripe, pubescent on inner face with shining hairs, somewhat spongy-thickened

dorsally at base in immature fruiting heads; receptacle alveolate, fimbriae ciliate; corolla 12–13 mm long; ligule 1.5 mm wide; teeth 0.25 mm long; corolla tube 2.5–3 mm long, pubescent with fine acicular hairs about 0.2 mm long; anther tube 4.5×1.5 mm dis.; appendages 0.5 mm long, acute; style branches 1.5 mm long, 0.1 mm wide, acute, yellow; achenes golden brown, 4.4–5 mm long, 0.5 mm wide, columnar, slightly attenuate to both ends, with slightly expanded pappus disk and calloused hollow base, subterete, about 16-striate, striae narrow, close, finely scabridulous; pappus white, 4.5–5.5 mm long, 1–2-seriate, rather stiff and brittle, persistent. Flowering June–July; flowers yellow.

Hieraciodes athoum O. Kuntze, Gen. 1: 345. 1891.

Known only from the type locality.

Monomorphic.

Greece: *Macedonia*, Hagion Oros Pen., Mt. Athos, on rocks, *Aucher-Eloy 3277* (Bo type, K, Ms); Mt. Athos, *Halacsy* in 1891 (Genoa); Mt. Athos, alpine, *Bornmüller and Sintenis 860* (K, PA, Fl); Mt. Athos, peak, *Orphanides* in 1862 (Bo); Mt. Athos, fully exposed, *Pichler* in 1873 (K, Bo); Mt. Athos, 1818–1939 m, *Heldreich* in 1862 (B); Mt. Athos, alpine, *Dimonic* in 1908, 1909 (B, US).

Relationship

C. athoa is closely related to *C. Guioliana* (q.v.), but the two are very distinct. A less close relationship between these two and *C. crocifolia* and *C. turcomania* is also indicated.

SECTION 11. MACROPODES

Relationships and distributions of the species

The 14 species in this section are characterized by a strong perennial woody caudex elongated into a taproot; by the basal leaves oblanceolate, petiolate, dentate or pinnatifid, and the few cauline leaves all or mostly bractlike; by the stem or stems mostly low, slender, 1–2-headed or rarely 3–4-headed; by the heads medium or small, the flowers yellow, the achenes of various colors, and the pappus white or yellowish-white.

Seven subgroups are recognized on the basis of closeness of morphological resemblance: (1) *C. Schachtii*, *C. pinnatifida*, *C. bithynica*; (2) *C. oreades*, *C. crocea*; (3) *C. tenerrima*, *C. xylorrhiza*; (4) *C. Hookeriana*, *C. Faureliana*; (5) *C. Robertioides*; (6) *C. heterotricha*, *C. armena*, *C. demavendi*; (7) *C. abyssinica*. The serial order of the first four subgroups is indicated by the comparative primitiveness of the most primitive member of each subgroup; but actually the relative degree of primitiveness of these species is very difficult to determine, since they vary with respect to different indices. The above order, therefore, is to some extent an arbitrary one.

(1) *C. Schachtii* stands first in the section in size of involucre and length of outer bracts. As in *C. tenerrima*, *C. xylorrhiza*, and *C. Hookeriana*, the inner bracts are but little changed in mature fruiting heads. Furthermore, the achenes, in both shape and ribbing, show more resemblance to those of *C. sibirica* than do those of any other species in the section. *C. pinnatifida* and *C. bithynica* are obviously close to *C. Schachtii*, and the three are distributed in the Balkan–Asia Minor area (fig. 131).

(2) *C. oreades* is an especially interesting species. Outside its own subgroup, the species to which it shows most resemblance is *C. bithynica*, and it is reasonable to assume that these two had a comparatively recent common ancestry. Their geographic distribution, therefore, is significant in that it agrees with the hypothesis that Central Asia was the center of origin of the genus. But *C. oreades* is so much closer to *C. crocea* that it is assumed to be one of its parents; and the distribution of these two species (fig. 131), as well as that of *C. Bungei* (fig. 162), is in line with this hypothesis. Furthermore, the extensive eastern and southern distribution of *C. crocea* coincides with the fact that it is a vigorous species under cultivation and with the hypothesis that it is an amphidiploid, the other parent being *C. Bungei*. Finally, *C. oreades* has been suspected (B. and S., 504: 30) of being one parent of *C. occidentalis*. The present occurrence of *C. oreades* as far east as the Semipalatinsk–Altai reg. (cf. Pavlov, 368) is well in line with this hypothesis, especially since *C. flexuosa*, the other putative parent, also occurs in that region.

(3) *C. tenerrima* and *C. xylorrhiza*, as indicated by size of heads and florets and the width and the ribs of the achenes, are not quite so primitive as *C. oreades* and *C. crocea*. Certain similarities between *C. tenerrima* and the more primitive species of sec. 8 suggest, however, some degree of relationship with that section. This is significant in view of the occurrence of these two species in Abyssinia. But such a relationship is not so definitely indicated for *C. xylorrhiza*. Both species resemble the other members of this section more than those of any other section. Their stations in N. Abyssinia are the southernmost limits of this section.

(4) *C. Hookeriana*, of the Great Atlas Mts., Morocco, and its close relative, *C. Faureliana*, of the Sahara Atlas, Algeria, represent the westernmost migration of the members of this section. Although the latter has been likened to *C. Robertioides* (Maire, Bull. Soc. d'Hist. Nat. Afr. Nord 29: 426. 1938), both of these species are actually closer to subgroups (1) and (2); and *C. Hookeriana*, in most respects, is

just about as primitive. On the principle that the more primitive members of a group will occur farthest from the center of origin, the present distribution of these two species is well in line with that of the other species in this section and with the hypothesis of a Central Asiatic origin for the genus.

(5) *C. Robertioides* certainly belongs in this section, but it is unique in its combination of small-sized heads and short outer bracts, together with the broad, many-ribbed achenes and especially in the ring of cilia borne just below the apex of the

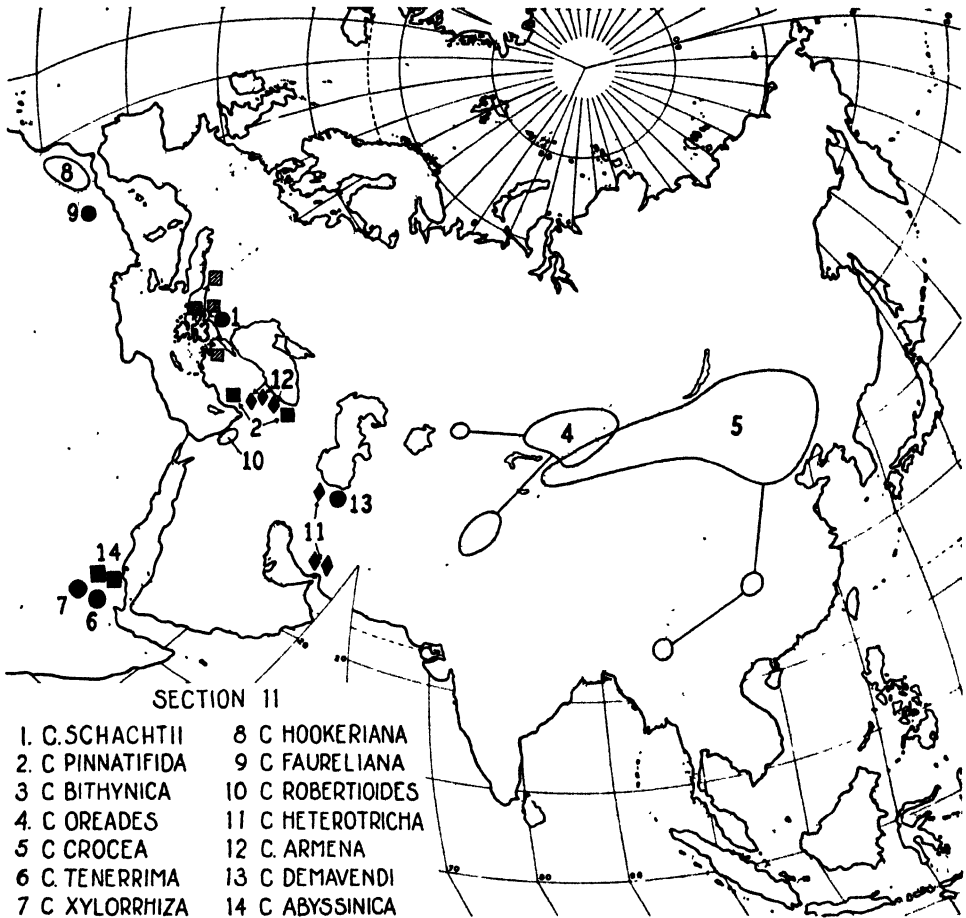


Fig. 131. Geographic distribution of the species in sec. 11. Single stations are indicated by solid circles, 2 known stations by solid squares, 3 stations by diamonds, and 4 stations by shaded squares. Based on Goode *Base Map 201 PC*. By permission of the University of Chicago Press.

achenes. It is endemic in the Liban Mts., Syria; but it occurs frequently over a considerable area in that region. Its very low stature, very slender stems, and small heads appear to be adaptations to extremely xerophytic conditions.

(6) *C. heterotricha*, *C. armena*, and *C. demavendi* comprise a close, distinctive group, and are somewhat more reduced in head size and other characters than the most primitive species in the section. They also exhibit a consistent geographic distribution, from E. Asia Minor to S. Persia.

(7) *C. abyssinica* exhibits most resemblance to *C. xylorrhiza* and is, no doubt, fairly close to that species in relationship. But it is much more reduced throughout and is, in fact, the most advanced species in this section.

These 14 species represent a remarkable range of distribution, from the Atlantic to the Pacific, across Eurasia in the general region of the 40th parallel of latitude, with 4 of the most primitive species occupying areas most distant from the assumed center of origin, and the fifth, *C. Schachtii*, existing as a local endemic near the center of the range. Thus, the distribution of the section as a whole is consistent with the hypothesis of a common origin in Central Asia followed by eastward, southward, and westward migrations (fig. 131).

Key to the Species of Section 11

- A Inner involucre bracts densely pubescent on inner face.
 - B Involucres 2–3 mm wide, with 7–9 inner bracts; corolla 8–10 mm long; pappus 3–4 mm long. Eritrea 101. *C. abyssinica*, p. 526
 - BB Involucres 4–9 mm wide, with 11–15 inner bracts; corolla 13–19 mm long; pappus 5–8 mm long.
 - C Leaves dentate to pinnately lobed, the lobes mostly entire, not spinulose on margin; inner involucre bracts without a dark median dorsal stripe; pappus setae rather coarse and stiff.
 - D Leaves without a very prominent midvein; involucres 8–10 mm long, with 7–8 outer bracts, the longest about $\frac{1}{3}$ as long as the inner; receptacle glabrous 91. *C. oreades*, p. 499
 - DD Leaves with a prominent pale or purplish midvein; involucres 11–14 mm long, with 8–13 outer bracts, the longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner; receptacle ciliate, the cilia caducous 92. *C. crocea*, p. 503
 - CC Leaves pinnately parted with acutely dentate segments, the lobes and teeth spinulose on margin; inner involucre bracts with a dark median dorsal stripe; pappus setae rather fine and soft 89. *C. pinnatifida*, p. 496
- AA Inner involucre bracts glabrous or rarely slightly pubescent on inner face.
 - E Outer involucre bracts imbricate, several of the outermost ovate, as wide as the inner bracts.
 - F Involucre bracts with a broad yellow margin, not ciliate on margin; heads 15–20-flowered; ligules yellow, suffused with red; pappus white, 6–8 mm long 98. *C. heterotricha*, p. 517
 - FF Involucre bracts without a broad margin, ciliate on the margin; heads 25–35-flowered; ligules yellow, without red; pappus white, tinged yellow, 4–7 (mostly 5–6) mm long 99. *C. armena*, p. 521
 - EE Outer involucre bracts not imbricate, lanceolate, lance-linear or linear, narrower than the inner bracts.
 - G Heads 11–19-flowered; achenes 1.3–1.6 mm wide, shortly ciliate below the pappus disk; pappus white, tinged yellow. Syria 97. *C. Robertioides*, p. 514
 - GG Heads 25–40-flowered; achenes 0.5–0.9 mm wide, not ciliate below the pappus disk; pappus white or tawny.
 - II Style branches green; pappus tawny; receptacle fimbriate, not ciliate. Abyssinia.
 - I Stems 1–2-furcate, the branches strict, with a narrow angle at the forks; heads half-nodding or semierect; outer involucre bracts 7–8 93. *C. tenerrima*, p. 507
 - II Stems 1-headed or 1–2-furcate, the branches spreading at a wide angle; heads erect; outer involucre bracts 10–12 94. *C. xylorrhiza*, p. 509
 - HH Style branches yellow; pappus white; receptacle ciliate or (*C. demavendi*) glabrous.
 - J Leaves sinuately denticulate; involucres 8–9 mm long, with 5–6 outer bracts; achenes stramineous 100. *C. demavendi*, p. 524

JJ Leaves coarsely dentate or pinnatifid; involucre 9–14 (mostly 10–12) mm long, with 8–10 outer bracts; achenes not stramineous.

K Outer involucre bracts all $\frac{1}{2}$ – $\frac{2}{3}$ as long as the inner; achenes 4.5–5 mm long, 10-ribbed, ribs narrow, sometimes with traces of additional ribs.....96. *C. Faureliana*, p. 513

KK Outer involucre bracts graduated from very short up to $\frac{1}{2}$ or $\frac{2}{3}$ as long as the inner; achenes 5–7.5 mm long, 15–20-ribbed or -striate.

L Ligules about 1 mm wide; anther tube 5 mm long; achenes with alternate ribs stronger, strongly spiculate.....95. *C. Hookeriana*, p. 511

LL Ligules 1.75–2.5 mm wide; anther tube 3–4 mm long; achenes with equal ribs or 4–5 stronger, smooth or finely spiculate.

M Stems 2–3-headed; involucre 9–12 mm long, 4 mm wide; achenes 5–6 mm long, 0.5 mm wide, 15-striate; pappus 4–5 mm long, very fine.....90. *C. bithynica*, p. 499

MM Stems 1-headed; involucre 12–14 mm long, 6 mm wide; achenes 7.5 mm long, 0.75 mm wide, 18–20 ribbed, with 4–5 stronger; pappus 6–7 mm long, medium-fine.....88. *C. Schachtii*, p. 494

88. *Crepis Schachtii* Bab.

Magyar Bot. Lap., 33: 3, 5, in adnot., 1934; Univ. Calif. Publ. Bot. 19: 403. 1941. (Fig. 132.)

Perennial, about 0.9 dm high; caudex woody, slender, tapering downward into a vertical taproot bearing fleshy fibers, covered with black bases of old leaves; leaves all caudical, ascending, up to 9 cm long, 2 cm wide, oblanceolate, obtuse or acute, unequally pinnately shallow-lobed or coarsely toothed, lateral segments \pm salient, reduced into a narrowly winged petiole with broader base, puberulent on both sides with fine pale gland hairs, glands brown; stems scapiform, bracteate, slender, terete, not fistulose, striate, \pm gland-puberulent, not much thickened near head, exceeding the leaves; head erect, medium, about 30-flowered; involucre campanulate, 12–14 mm long, 6 mm wide near base in fruiting head, densely pubescent with long pale glandulose setaceous hairs; outer bracts 10, unequal, the longest $\frac{2}{3}$ as long as inner bracts, lanceolate, acute, white-ciliate at apex; inner bracts 15, in 2 series nearly equal, lanceolate, acute or acuminate, white-ciliate at apex, glabrous within, slightly thickened at base in immature fruiting head; corolla about 14 mm long; ligule 2.5 mm wide; teeth 0.25–0.35 mm long, triangular-obtuse; corolla tube 4 mm long, bearing very few short (0.1–0.2 mm long) stout 2-celled simple or furcate trichomes; anther tube 3.75×1.3 mm dis.; appendages 0.6 mm long, rather broad, sagittate-acute; filaments 1 mm longer; style branches 1.25–1.75 mm long, 0.15 mm wide, gradually attenuate upward, yellow; achenes grayish-brown, 7.5 mm long, 0.75 mm wide, straight or slightly curved, subterete, gradually and rather strongly attenuate to the pale expanded pappus disk, equally constricted above the hollow calloused base, 18–20-ribbed, ribs unequal, 4–5 stronger, all narrow, rounded, finely spiculate near apex; pappus white, 6–7 mm long, conspicuously exceeding the involucre, 1-seriate, setae 30–50 μ wide at base, rather stiff, persistent. Flowering July; flowers yellow. Chromosomes, $2n = 10$.

Known only from the type locality.

Monomorphic.

Bulgaria (E. Macedonia): Mt. Ali-Botusch, dry places on calcareous rocks, 1300 m, *Schacht* in 1932 (Sofia). Original description, with illustration and fragments from the type (UC).



Fig. 132. *Crepis Schachtii*, from type (Sofia): a, plant, $\times 1$; b, leaf, upper face, $\times 1$; c, fruiting head and peduncle, $\times 2$; d, floret lacking ovary, $\times 4$; d', detail of ligule teeth, $\times 8$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g-i, 2 achenes and a pappus seta, $\times 8$; j, somatic chromosomes from hort. genet. Calif. 3240 (grown from seeds collected at type locality by Mr. Schacht and sent by Dr. B. Stefanoff, Sofia).

Relationship

Crepis Schachtii stands first in this section on the basis of size of involucre and length of the outer bracts. Although it shows considerable resemblance to *C. bithynica*, especially in the root and leaves, it is actually closer to *C. pinnatifida* in the scapiform stem and larger florets and achenes. In karyotype it is intermediate between *C. bithynica* and *C. Raulini*.

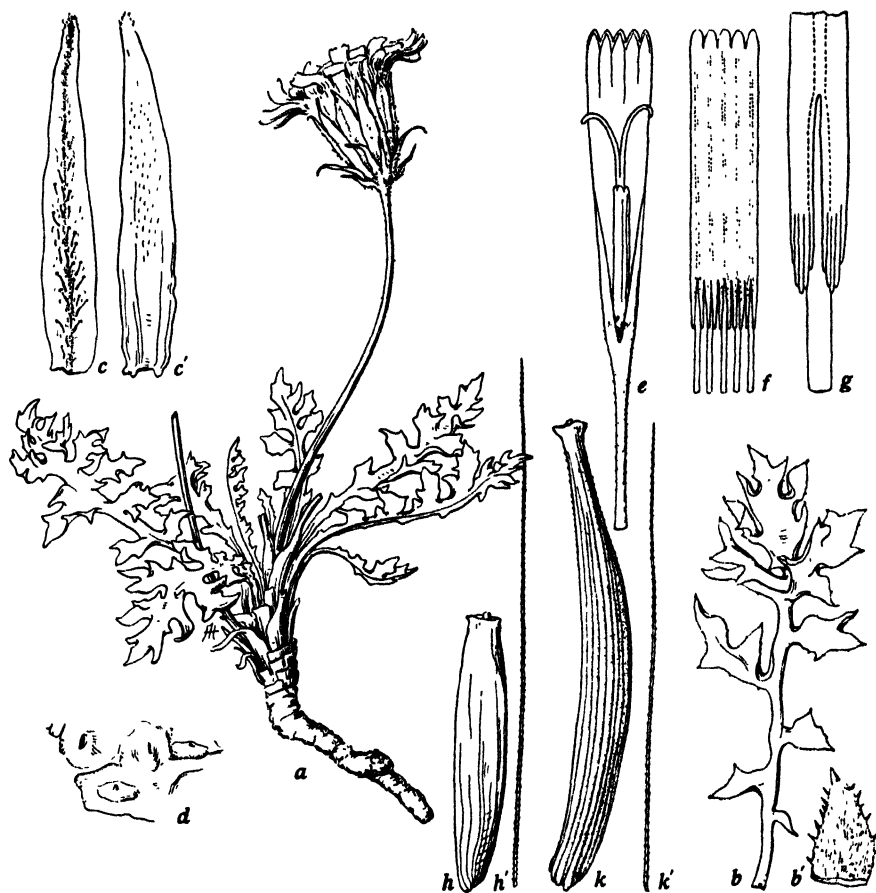


Fig. 133. *Crepis pinnatifida*, from Huet du Pavillon in 1853 (K), except *k, k'*, from Balansa 648 (G): *a*, plant, $\times 1$; *b*, leaf, $\times 2$, *b'*, tip of a leaf lobe, $\times 8$; *c, c'*, inner involucre bract, outer and inner faces, $\times 4$; *d*, detail of receptacle, $\times 25$; *e*, floret lacking ovary, $\times 4$; *f*, anther tube, $\times 8$; *g*, detail of appendages, $\times 32$; *h, h'*, immature achene and a pappus seta, $\times 8$; *k, k'*, nearly mature achene and a pappus seta, $\times 8$.

89. *Crepis pinnatifida* (Willd.) Froel.

Ex DC., Prod. 7: 167. 1838. (Fig. 133.)

Perennial, 0.3–0.8 dm high; caudex woody, vertical, 1–6 cm long, 0.5–2 cm wide at crown, simple or divided, gradually attenuate into a long vertical or oblique woody taproot, covered with brown bases of old leaves, leafy at crown; leaves all caudical, numerous, up to 7 cm long, 2 cm wide, oblanceolate, acute, pinnately parted with close or remote acutely dentate lobes, the lobes and teeth mucronate and corneous-spinulose on margin, attenuate into a short winged petiole, broader

at base, densely canescent-tomentose and sometimes setulose with yellowish spinulose setules or finely gland-pubescent; scapes 1–4, erect or sinuate, slender, terete, densely canescent-tomentose, sometimes shortly setulose with or without glands, slightly thickened near base of head; heads erect, medium, 30–60-flowered; involucre campanulate, 12–14 mm high, 6–9 mm wide at middle in fruit, densely canescent-tomentose; outer bracts 7–9, unequal, longest $\frac{1}{2}$ as long as the inner, lanceolate, acute or acuminate; inner bracts 11–15, lanceolate, acuminate, rounded at the white-ciliate yellowish apex, with dark brown or black median dorsal stripe bearing very short gland hairs, densely and shortly appressed-pubescent on inner face, becoming dorsally convex, \pm carinate and obscurely spongy-thickened at base in fruit; receptacle areolate, glabrous; corolla 14–16 mm long; ligule about 2 mm wide; teeth 0.75 mm long; corolla tube 5–6 mm long, beset with minute conical 2-celled trichomes; anther tube about 5×1 mm dis.; appendages 0.75 mm long, oblong, acute; style branches about 2 mm long, 0.1 mm wide, yellow; achenes (not fully mature) dark brown or nearly black, 7.5–9.5 mm long, 1–1.2 mm wide, subterete (?), more strongly attenuate upward, 0.3–0.5 mm wide just below the expanded pappus disk, narrowed to the yellowish strongly calloused base, about 20-ribbed, ribs close, narrow, rounded, strongly spiculate near the apex; pappus white or dusky, yellowish near base, 6–8 mm long, 2-seriate, setae unequal, outer series coarser, $30\text{--}55\mu$ wide at base, rather soft, persistent. Flowering July–Aug.; flowers yellow.

Hieracium pinnatifidum Willd., Sp. Pl. 3(3): 1560. 1804, non *C. pinnatifida* Willd., *op. cit.*, 1604 = *C. capillaris*.

Hieraciodon pinnatifidum O. Kuntze, Gen. 1: 346. 1891.

Asia Minor, mountains of E. and S.-central Turkey.

The type, in Herb. Willd. (Berol.) n. 14661–1, is labeled “Dens Leonis armenus, tenuissime divisus, tomentosus et incanus,” and is probably the type of Tournefort (Cor. Inst. 35. 1703). The type is fragmentary, comprising one leaf and a scape bearing a mutilated head with a few florets and immature achenes; but this material, together with Willdenow’s description, is sufficient to establish the species beyond question and to enable the definite identification of the specimens cited below.

Monomorphic.

Turkey: “armenus” *file* Tournefort (BW) type; “Armenia,” Mt. Palanten Ken, above Erzerum, 2424–2727 m, *Huet du Pavillon* in 1853 (Bo, K); Taurus Mts., *Kotschy 320* (Bo, Genoa, Mo); E. Taurus, alpine reg., above Boulgarmaden, *Balansa 1023* in 1855 (Bo, UCf, G); Tchihatchef, *Calvert* in 1854 (Bo.).

In addition to the above, the following specimens have been seen but cannot, without reexamination, be cited with full confidence under this species. It is possible that part or all of them are *C. dioritica*. **Asia Minor:** Cappadocia (Argaeus), 2800 m, *Siehe 231* in July, 1898 (UWG); Argaeus, Erdschias-dagh, in the N. crater, 2400–2900 m, *Lederbauer* in July, 1902 (UWG); Cilicia. Kizil Deps, 2800 m, calcareous soil, *Siehe 246* in Aug., 1895 (B).

Relationship

Crepis pinnatifida, although superficially resembling *C. dioritica*, is very distinct from that species in the deeply penetrating taproot, in the larger flower heads with narrower outer involucre bracts, in the inner bracts pubescent on inner face, and in the larger florets and longer pappus. Probably the achenes also differ, but mature achenes of *C. dioritica* have not been seen. *C. pinnatifida* stands between *C. Schachtii* and *C. bithynica* on the basis of degree of reduction in size of involucre, although its florets and achenes are slightly larger than those of *C. Schachtii*.

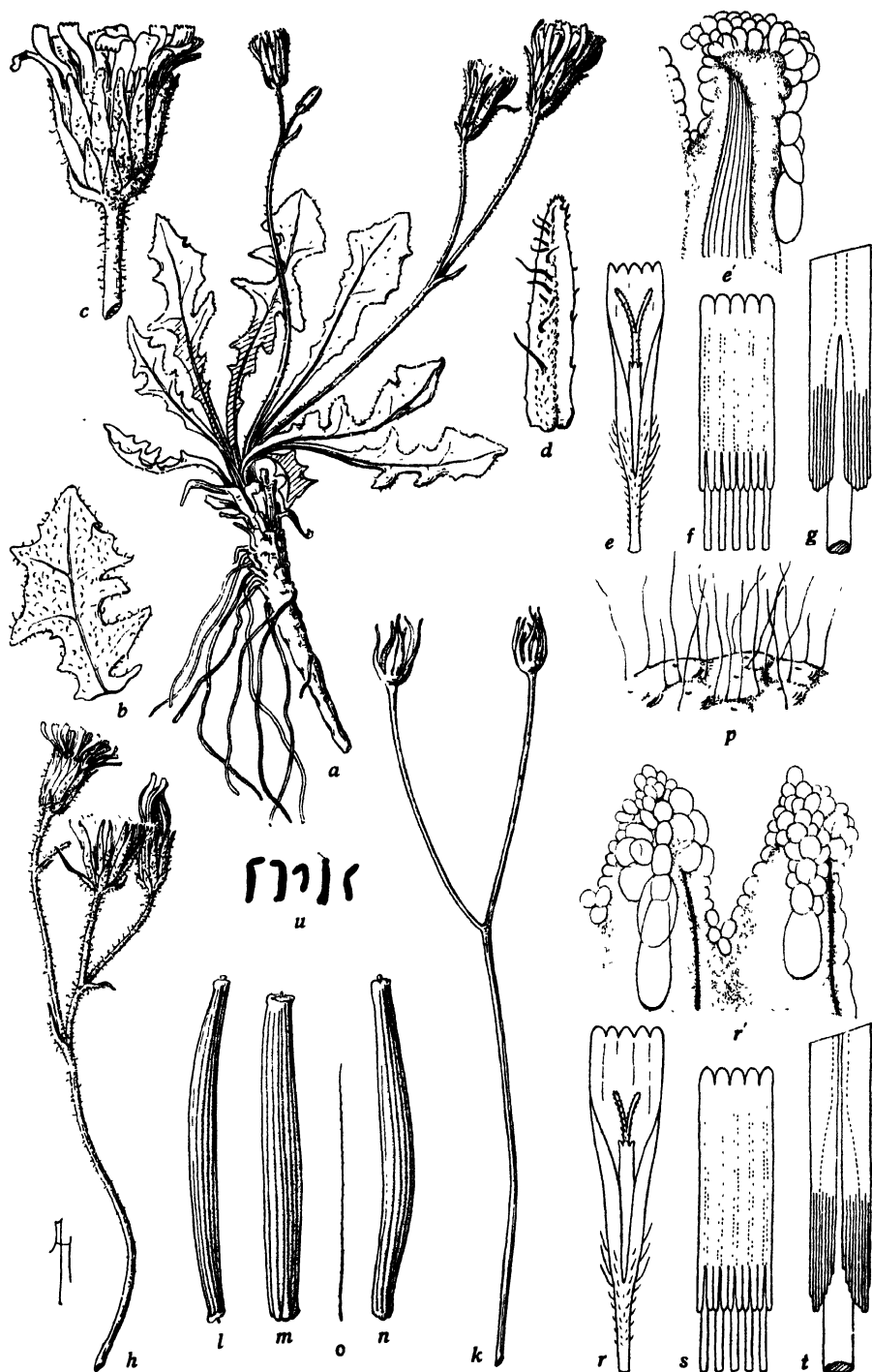


Fig. 134. *Crepis bithynica*, a, b, from Pichler 172 (B); c-g, from type (Bo); h-p, from Stefanoff in 1929 (UC 470089); r-u, from Georgieff in 1932 (UC 489443): a, plant, $\times 1$; b, part of leaf, $\times 2$; c, head, $\times 2$; d, inner involucre bract, outer face, $\times 4$; e, detail of ligule tooth, lateral view, $\times 50$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, stem with 3 young heads, $\times 1$; k, stem with fully developed heads, $\times 1$; l-o, 3 achenes and a pappus seta, $\times 8$; p, detail of receptacle, $\times 25$; r, floret lacking ovary, $\times 4$; s, detail of ligule teeth, outer face, $\times 50$; t, anther tube, $\times 8$; u, detail of appendages, $\times 32$; u, somatic chromosomes (plants grown from seeds collected by T. Georgieff on Mt. Pirin in 1932), $n = 5$, $\times 1250$.

90. *Crepis bithynica* Boiss.

Diag. Pl. Orient. Nov. ser. 1, 4: 29. 1844. (Fig. 134.)

Perennial, 0.5–1.2 dm high; caudex woody, slender, tapering downward into a vertical or oblique taproot bearing strong fleshy fibers and sometimes the remains of old petioles, crown covered with bases of old leaves; leaves all caudical, numerous, ascending, up to 10 cm long, 1.3 cm wide, spatulate and rounded-obtuse or oblanceolate and acute, pinnately shallow-lobed or dentate, attenuate into the narrowly winged petiole with broader base, pubescent on both sides with fine short yellow glandular or glandless hairs; stems 1–4, simple or 1–2-furcate, bracteate at bifurcations, flexuous, striate, shortly gland-pubescent or glabrate below; peduncles 1.5–10 cm long, gland-pubescent; heads medium, erect, 30–40-flowered; involucre campanulate, 9–12 mm high, 4 mm wide near base in mature heads, densely pubescent with short glandular and glandless hairs, sometimes tomentulose at base; outer bracts 10, unequal, longest $\frac{1}{2}$ as long as inner bracts, lanceolate, acute; inner bracts 12–14, in 2 ranks, innermost broadly scarious-margined, lanceolate, acute, ultimately spongy-thickened confluent with the thickened base, remaining erect, glabrous within; receptacle areolate-ciliate, cilia up to 0.75 mm long, very fine, white, crinkled; corolla 10–12 mm long; ligule 1.75–2.5 mm wide, dorsally pubescent below; teeth 0.25–0.35 mm long, triangular-obtuse, very conspicuously crested; corolla tube 2.5–3 mm long, pubescent with 2–4-celled hairs 0.05–0.9 mm long; anther tube (3.5)4.25–1.25 mm dis.; appendages 0.7–0.8 mm long, rather broad, \pm sagittate; filaments 1 mm longer; style branches 1.75 mm long, 0.15 mm wide, gradually attenuate, yellow; achenes pale greenish-yellow, 5–6 mm long, 0.5 mm wide, straight or somewhat curved, terete or dorsoventrally subcompressed, slightly attenuate to both ends, with slightly expanded pappus disk and hollow calloused base, 15-striate, glabrous; pappus white, 4–5 mm long, 2-seriate, very fine, soft, persistent. Flowering July–Aug.; flowers yellow. Chromosomes, $2n = 10$.

Hieraciodes bithynicum O. Kuntze, Gen. 1: 345. 1891.

N.W. Asia Minor and the Balkan Pen., higher montane regions on calcareous formations. 1500–2100 m alt.

The type material and other plants from the type region correspond closely with specimens from the Balkan Pen., even in certain minute details (see fig. 134), and the minor differences observed are such as might be expected to occur among plants of this species in either of the two regions.

Asia Minor: Brusa, Olympus (Keshish-Dagh), upper part, Boissier in 1842 (Bo, UCf) type; *ibid.*, on the highest N. shoulder, Pichler 79 (Bo); *ibid.*, on the highest peak, Pichler 172 (Fl, B, UCf, K). **Balkan Peninsula:** Greece, Thessaly, Mt. Olympus, alpine pastures among the peaks, Heldreich 2484 (Bo); Bulgaria (Macedonia), Mt. Pirin, Kutela, stony places on chalk, Georgieff in 1932 (UC); *ibid.*, Mt. Pirin, Bajovi Dupki, among calcareous rocks, Stefanoff in 1929 (UC); W. Bosnia, Sator planina, S. slopes, Janchen in 1904 (UWH, UWG).

Relationship

C. bithynica, first determined as *C. armena* by Boissier, somewhat resembles that little-known species in size and habit. It is much closer, however, to *C. Schachtii*, *C. pinnatifida*, and *C. heterotricha*, and it is intermediate between the first two and the last in size of involucre, particularly in the outer involucre bracts.

91. *Crepis oreades* Schrenk

Enum. Pl. Nov. 2: 32. 1841. (Pl. 9, d. Fig. 135.)

Perennial, forming small tufts; caudex 1.5–3 cm long, simple, 0.5 cm wide, or 2–6-furcate and up to 3 cm wide, prolonged into a slender vertical or oblique tap-

root bearing adventitious buds; caudical leaves erect or ascending, 2–6 cm long, up to 1 cm wide, oblanceolate, obtuse or acute, sinuate-denticulate, runcinate-pinnatifid or pinnately parted with triangular or lance-linear lateral segments, attenuate into a winged or scarcely winged petiole 1–2 cm long with broader base, canescent-tomentulose or glabrescent, not hispidulous (in m.v. 1, up to 8 cm long and 2.5 cm wide, pinnately parted into remote narrow acute segments, canescent-tomentose, \pm hispidulous, sometimes glandular); cauline leaves petiolate or sessile, linear, filamentous or bractlike (in m.v. 1, sometimes lanceolate, pinnate); stems 1–5, scapiform, 1.2–1.7 dm high, bracteate, terete, striate, tomentulose, fistulose, (in m.v. 1, simple or furcate, 0.8–1.1 dm high, branches pedunculate); peduncle tomentose and sometimes hispidulous near head, not much thickened; heads erect, medium, many-flowered; involucre 9–10 mm high, campanulate; outer bracts 7 or 8, unequal, longest about $\frac{1}{3}$ as long as inner bracts, lanceolate, acute, tomentose or glabrescent, sometimes hispidulous; inner bracts 12–14, lanceolate, acute or obtuse, ciliate at apex, in 2 ranks, the inner ones scarious-margined, \pm tomentose, often pubescent with dark setiform glandless or glandular hairs, ventrally pubescent with short hairs, the amount of dorsal thickening in fruiting heads not seen; receptacle areolate, glabrous; corolla 15–18 mm long; ligule 1.75–2.5 mm wide; teeth 0.3–0.5 mm long; corolla tube 4.5–6 mm long, sparsely or densely beset with coarse 2-celled or stalked acicular hairs up to 0.2 mm long; anther tube (3) 4.5×1 (1.25) mm, yellow; appendages 0.7–0.8 mm long, oblong, truncate-oblique or acute; filaments 0.4–0.5 mm longer; style branches 1.5–2.5 mm long, 0.15 mm wide, yellow; achenes not seen;¹ pappus white, 5–6 mm long, 2-seriate, rather coarse, stiff but pliable, coming away in clumps, persistent. Flowering June–Aug.; flowers yellow. Chromosomes, $2n = 8$.

Hieraciodes oreades O. Kuntze, Gen. 1: 346. 1891.

Mountains of Central Asia, from the Tarbagatai Range in W. Mongolia, Dzungaria, and S. Siberia, southwestward to the Pamirs, and westward in Kazakstan (formerly the Kirghiz Republic) to the Ulutau Mts., in the S.E. Turgai reg.; alpine summits and dry places at lower altitudes.

Specimens of the form known as var. b, *simplex* of Schrenk (*op. cit.*, 33) are labeled *Crepis oreades* Schrenk without varietal designation in *Schrenk 333* (K, ex Herb. Hort. Petrop.), and on the same sheet are exactly similar specimens, *Schrenk 218*, labeled var. *simplex*, Attagai-Assu, which is the type locality for this variant in the original description. This form is, therefore, accepted as the type of the species. Attagai-Assu, acc. to C. A. Meyer, in herb., is in the Tarbagatai Range. For m.v. 1 (= var. b, *cinerascens*), the type locality is Dschabyk Mts.; and, acc. to Fedtschenko, Mt. Dschabyk is in the Dzungarian Alatau, where the typical form has also been collected. The type region for the species is, therefore, W. Dzungarian Mongolia; and it is worth noting in passing that this northeastern extremity of the range of this species, as at present known, approaches rather near to the known western limit of *C. Bungei*. It should be noted also that, if C. A. Meyer's label (in herb. Boiss.) giving Mt. Ulutau as the locality for one collection of the typical form of *C. oreades* is correct, the range of the species is extended over 1,000 miles westward; and it would be just as likely to extend similarly through the mountains eastward. Furthermore, the very indefinite locality given for the specimens of this species in herb. DC. by Turczaninow, viz., "Chinese Mongolia," may extend the

¹ The achenes of this species have not been seen by the author; those which were received during the absence of the author in 1930 were all sown. Only one plant was obtained and it failed to produce fruits. Schrenk (*loc. cit.*) states that the achenes are not attenuate into a beak.



Fig. 135. *Crepis orcadetes*, a-f, from Alatau, Meyer in 1842 (Bo); g-i, from Attagai-Assu, Schrenk #18 (K); k-t, from Tarbagatai, Schrenk (Bo); u, from hort. genet. Calif. 2981 (grown from seeds received from Lepsinsk dist., Dzungaria, through Dr. M. Navashin): a, plant, $\times \frac{1}{2}$; b, c, caudical leaves, $\times 1$; d, head, $\times 2$; e-f, inner involucre bracts, outer and inner faces, $\times 4$; g, floret lacking ovary, $\times 4$; g', detail of ligule teeth, $\times 25$; h, anther tube, $\times 8$; i, detail of appendages, $\times 32$; k, plant, $\times \frac{1}{2}$; l-n, caudical leaves, $\times 1$; o, head, $\times 2$; p-q, inner involucre bracts, outer and inner faces, $\times 4$; r, floret lacking ovary, $\times 4$; r', detail of ligule teeth, $\times 25$; s, anther tube, $\times 8$; t, detail of appendages, $\times 32$; u, somatic chromosomes, $n = 4$, $\times 1250$.

range of this species considerably farther east. Hence it is not unlikely that the two species overlap somewhere in the Altai reg.

The foregoing conjectures regarding the distribution of this species have recently been verified by Pavlov (368), whose discussion of this species has been translated as follows: "An endemic species of mountainous Turkestan, found also in Kazakhstan in the southeastern corner of the Turgai region (northern and western borders of the Ulutavsk Mts.). It is also found in the mountains of southern Kazakhstan, eastward as far as the Semipalatinsk Altai, and in Turkestan as far as Zeravshan and Pamir. In these regions the plant is quite common, being found at various elevations and in isolated mountain systems; it varies somewhat with weak, intergrading forms. Of these, spread exclusively¹ in the Ulutavsk district, is var. *simplex* Schrenk, distinguished by low, 1-headed scapes and nearly entire, glabrous or almost glabrous leaves. Further to the south is spread the more robust var. *cinerascens* Schrenk, with many-headed inflorescence, pinnate leaves, and gray tomentum on leaves, peduncles and involucres." So far as geographic distribution is concerned, therefore, there is no obstacle to the hypothesis that *C. oreades* hybridized with *C. Bungei* and thus made possible the amphidiploid *C. crocea*.

Dzungaria: Attagai-Assu, Schrenk 218 (K, ex Herb. Hort. Petrop.) isotype; Ulutau (= Dzungarian Alatau acc. to Fedtschenko, Beih. Bot. Centralb. 40: 205), Schrenk 333 (K, ex Herb. Hort. Petrop.); without definite locality, Schrenk teste Trautv. (K, G, ex Herb. Hort. Petrop.) m.v. 1; *ibid.*, Schrenk (G); Tarbagatai Range, alpine summit, Schrenk (Bo, ex Herb. Bunge); Tarbagatai Range, dry place, Schrenk (Bo, ex Herb. Bunge) m.v. 1; Tarbagatai Range, summit (Attagai-Assu), C. A. Meyer in 1841 (Bo); Ulutau (the occurrence of this species in the Ulutau Mts. has been verified, and the label does not state "*Songorei*," as in Schrenk's collections; cf. date of next citation), C. A. Meyer in 1842 (Bo, UCf); Alatau Mts., dry peak, C. A. Meyer in 1841 (Bo, UCf) m.v. 1. "Chinese Mongolia": in a rather sandy place, Turcsaninow in 1831 (DC, Prod. vii: 168, n. 36, UCf). Fedtschenko (Beih. Bot. Centralb. 40: 205) lists the following collections without specifying the forms represented: Dzungarian Alatau: Sairam, Südo-stufer. Pamiroalai: Seraws-chan, Alai-Kette, O. and B. Fedtschenko; Transalai-Kette, O. and B. Fedtschenko. Pamir: Kok-dshar, Chorew.

Minor Variant of *C. oreades*

1. (*C. oreades* var. *cinerascens* Schrenk, *op. cit.*, 33.) Differs from the typical form of the species mainly in the lower stature and broader leaves with heavier tomentum, and in some specimens the leaves and stems are \pm hispidulous. Characterized by having the leaves pinnately parted with remote narrow and sometimes dentate lateral segments, but the typical form sometimes has pinnately parted leaves also. Floral characters and pappus are closely similar to those of the typical form. Achenes not seen. Two of the 4 specimens seen were collected in dry places and the variant may be merely an ecad. It seems more probable, however, that it differs genetically from the typical form in its peculiar combination of larger leaves and shorter stems. The statement of Herder (198) that this variant is not different from *C. crocea* is in error. Schrenk (Bo), dry place, Tarbagatai Range, Dzungaria; Schrenk (K, G), without definite locality, Dzungaria; C. A. Meyer in 1841 (Bo), dry peak, Alatau Mts.

Relationship

Crepis oreades is classified under *Eucrepis* by its author, who, acc. to Trautvettero (Bull. Soc. Nat. Mosc. 39[2]: 388. 1866), collected a fruiting specimen. The evidence from chromosome morphology strongly indicates that it is one of the two species which, through natural hybridization followed by amphidiploidy, gave rise to *C. crocea*. It is well known that amphidiploid hybrids derived from closely related species tend to be sterile and to produce extremely variable progeny, whereas similar hybrids between distantly related species are more apt to be highly fertile and fairly constant. From the author having grown 3 different accessions of *C. crocea*, which were collected at different places, and having found them closely similar to one another, we may infer that this species is fairly constant under natural

¹ Obviously an error, since the type locality for var. *simplex* is Attagai-Assu in Dzungaria.

conditions and that its parental species were not closely related. The plants are also highly fertile. The tendency which has been observed in *C. crocea* to have the inner involucre bracts definitely spongy-thickened and confluent with the thickened base in some specimens is good reason for assuming a similar tendency in *C. oreades*. This species is closest perhaps to *C. bithynica*, from which it is easily distinguished by having the involucre bracts pubescent within and the florets longer. *C. oreades* may also represent one of the ancestral stocks that entered into the origin of *C. occidentalis* (q.v.)

92. *Crepis crocea* (Lamk.) Babc.

Univ. Calif. Publ. Bot., 19: 400. 1941. (Pl. 9, a-c. Fig. 136.)

Perennial, mat-forming, by spreading from root sprouts; caudex 5–15 mm long and about as wide, simple or 1-furcate, prolonged into a slender vertical or oblique taproot from which adventitious buds arise; caudical leaves up to 7 cm long, 2 cm wide, oblanceolate, acute, sinuate-dentate, with acute teeth, or runcinate-pinnatifid, with irregular narrow acute segments, or pinnately parted, the segments triangular to linear, attenuate into a short winged petiole with broader clasping base, the midrib conspicuous, white or pale purplish on both sides, like stem canescent-tomentulose or glabrescent; cauline leaves similar or sessile, linear, acuminate, uppermost bractlike; stems 1–4, terete, striate, fistulose, (0.2)1–2(3.5) dm high, simple and leafy or bracteate, or 1–5-furcate, often branched from near base, branches remote, long, strict or arcuate, usually pedunculate, rarely 2–3-headed; peduncles \pm tomentulose, often shortly gland-pubescent or -hispidulous, \pm thickened and often with several bracts near head; heads erect, medium, many-flowered; involucre 11–14 mm high, 5–7 mm wide near base in anthesis, campanulate; outer bracts 8–13, unequal, longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as inner bracts, lance-linear, acuminate, like inner bracts canescent-tomentose and sometimes pubescent or hispidulous, \pm scarious, becoming reflexed; inner bracts 14, lanceolate, obtuse and ciliate at apex, in 2 or 3 ranks, inner ones broadly scarious-margined, gland-pubescent or setaceous, sometimes with long dark glandless and shorter glandular hairs mixed, becoming \pm carinate and spongy-thickened dorsally, this often obscure but sometimes evident and confluent with the thickened base, ultimately reflexed or remaining erect, ventrally pubescent with coarse yellow or white hairs; receptacle areolate, subfimbriate, fimbriae finely ciliate, cilia caducous; corolla 13.5–19 mm long; ligule 1.5–2.25 mm wide; teeth 0.25–0.65 mm long, obtuse; corolla tube 4.5–6.5 mm long, sparsely beset with 2-celled acicular hairs up to 0.2 mm long; anther tube yellow, (4)5.75 \times 1(1.5) mm dis.; appendages 0.75–1.1 mm long, oblong; filaments equal, 0.4–0.75 mm longer; style branches (1.5)2.5–3.25 mm long, 0.15 mm wide, yellow; mature achenes dark purple or black, yellow at summit and base, 5–6 mm long, 1 mm wide, \pm curved or nearly straight, fusiform, more strongly attenuate upward in most, constricted above the calloused hollow base, 18-ribbed, ribs nearly equal, rounded, finely spiculate under lens; pappus white, copious, 7–8 mm long, 3–4-seriate, rather stiff but pliable, persistent. Flowering May–Sept.; flowers yellow. Chromosomes, $2n = 16$.

Hieracium croceum Lamk., Encycl. Meth. 2: 360. 1786.

Crepis Gmelini var. *grandiflora*, foliis magis dissectis, Tausch, Flora, 11 (Erg.): 78. 1828.

C. aurea var. *crocea* Froel., ex DC, Prod. 7: 168. 1838.

C. Pallasii Turcz., Bull. Soc. Nat. Mosc. 11: 96. 1838.

C. Turczaninowii C. A. Mey., ex Turcz., Bull. Soc. Nat. Mosc. 21: 110. 1848.

H. polytrichum var. *apricum* Bunge, Enum. Alt. 81, fide Ledeb., Fl. Ros. 2: 825. 1844–1846.

H. crocatum Bunge, ined., fide Ledeb., loc. cit.

Berinia crocea Sch. Bip., Pollichia, 22–24: 317. 1866.

Hieraciodes croceum O. Kuntze, Gen. 1: 345. 1891.

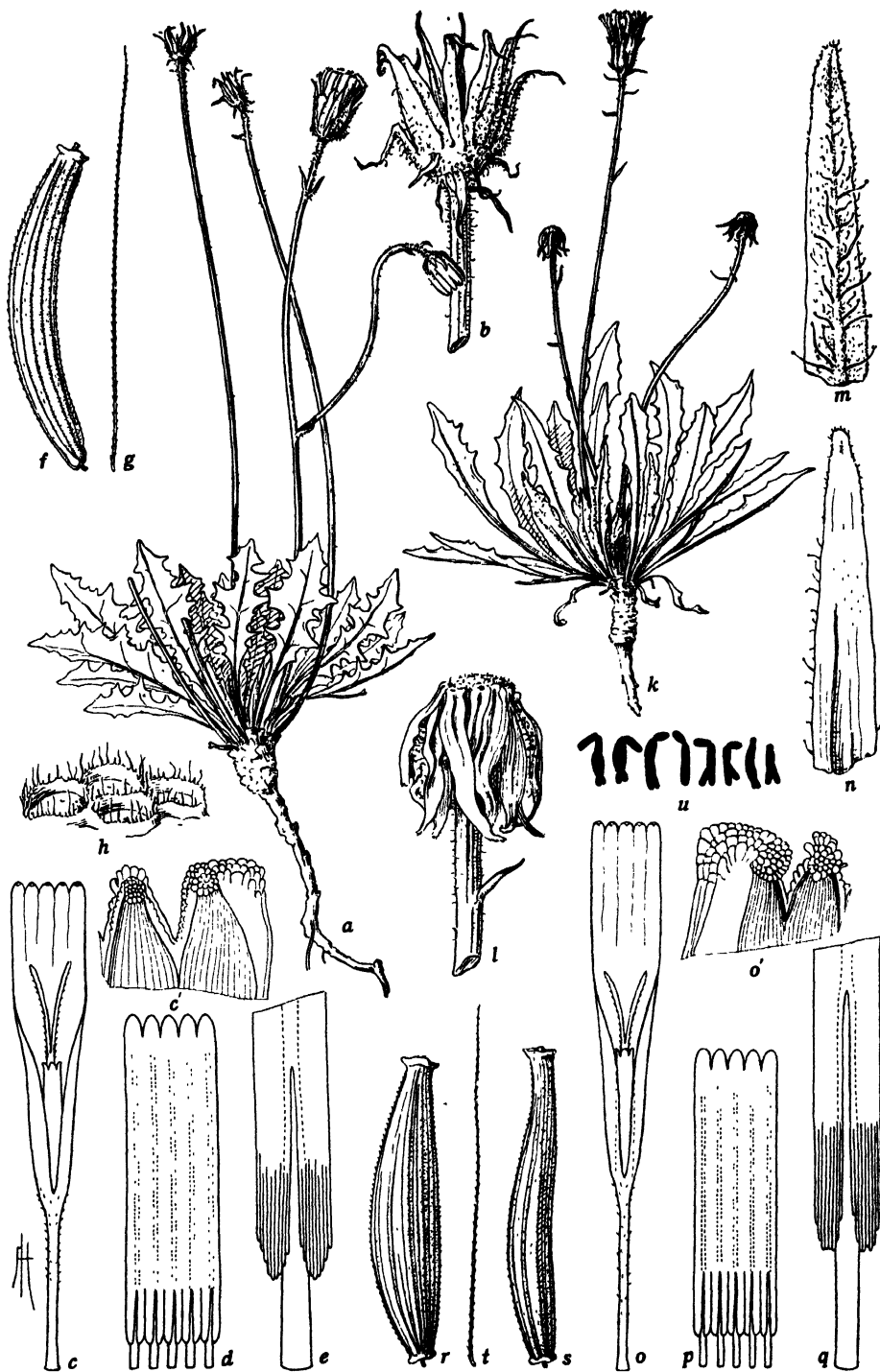


Fig. 136. *Crepis crocea*, a-g, from Smith 142 (Upsala); h, from Pavlov 1499 (Mosc); k-q, from hort. genet. Calif. 2174 (UC 499375); r-u, from hort. genet. Calif. 2352 (UC 494357): a, plant, $\times \frac{1}{2}$; b, old head, $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule teeth, $\times 25$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, g, achene and a pappus seta, $\times 8$; h, detail of receptacle, $\times 25$; k, plant, $\times \frac{1}{2}$; l, old head with bracts reflexed, $\times 2$; m, n, inner involucre bract, outer and inner face, $\times 4$; o, floret lacking ovary, $\times 4$; o', detail of ligule teeth, $\times 25$; p, anther tube, $\times 8$; q, detail of appendages, $\times 32$; r-t, 2 achenes and a pappus seta, $\times 8$; u, somatic chromosomes, $2n = 16$ ($x = 4$), $\times 1250$.

TABLE 14
SYNOPTICAL COMPARISON OF THE CHARACTERS DISTINGUISHING *CREPIS CROCEA*
FROM ITS PUTATIVE PARENTS, *C. BUNGEI* AND *C. OREADES* (TYPICAL FORM)

Character	<i>C. crocea</i>	<i>C. Bungei</i>	<i>C. oreades</i>
Caudex	5-15 mm long 3-15 mm wide	5-10 mm long 4-8 mm wide	15-30 mm long 5-30 mm wide
Rosettes	persistent	dying away	?
Leaves (maximum)	7 cm long; 2 cm wide	10 cm long; 1.5 cm wide	6 cm long; 1 cm wide
Stems	1-4, simple or branched from near base, 0.2- 3.5 dm high	one, 1.3-3 dm high, co- rymbosely branched above middle	1-5, scapiform, 1.2-1.7 dm high
Involucre	11-14 mm high	9-11 mm high	9-10 mm high
Outer bracts	8-13, longest $\frac{1}{3}$ to $\frac{1}{2}$ as long as inner ones	ca. 10, nearly $\frac{1}{2}$ as long as inner ones	7 or 8, longest $\frac{1}{3}$ as long as inner ones
Inner bracts	ca. 14; dorsally glandu- lose or setaceous, \pm carinate and spongy- thickened; ventrally pubescent	12-16; dorsally glandu- lose, \pm carinate and spongy-thickened; ventrally pubescent or glabrescent	12-14; dorsally pubes- cent or setaceous, becoming carinate ? or thickened ?; ven- trally pubescent
Receptacle	subfimbriate, finely ciliate	areolate, glabrous or with occasional very fine cilia	areolate, glabrous
Corolla	13.5-19 mm long	14-17.5 mm long	15-18 mm long
Ligule	1.5-2.25 mm wide	2-2.75 mm wide	1.75-2.5 mm wide
Ligule teeth	crested and hooded	crowned and hooded	capitate or crested, not hooded
Corolla tube	4.5-6.5 mm long, sparsely hairy, hairs coarse, up to 0.2 mm long	4-6 mm long, glabrous or sparsely hairy, hairs fine, less than 0.1 mm long	4.5-6 mm long, sparsely or densely hairy, hairs coarse, up to 0.2 mm long
Anther tube (opened out)	(4)5.75 \times 1(1.5) mm	(4)5 \times 1.25 mm	(3)4.5 \times 1(1.25) mm
Filaments	short, extending 0.4-0.75 mm beyond append- ages	long, extending 1-1.5 mm beyond append- ages	short, extending 0.4-0.5 mm beyond append- ages
Appendages	0.75-1.1 mm long	0.6-1.0 mm long	0.7-0.8 mm long
Style branches	1.5-3.25 mm long	2.5-3.5 mm long	1.5-2.5 mm long
Achenes	5-6 mm long, 1.0 mm wide, 18-ribbed	4-5 mm long, 0.75 mm wide, 10-12-ribbed	?
Pappus	7-8 mm long; 3-4-seriate	7-8 mm long; 2-seriate	5-6 mm long; 2-seriate

Authentic specimens of *H. croceum* Lamk. are compared with Gmelin's figure (Fl. Sib. II tab. viii, f. 1) in plate 9.

Central Asia, in S. Siberia from the Altai reg. eastward to Transbaikalia, southward into Manchuria, N. China, Mongolia, Dzungaria, and N.E. Tibet; mountain slopes, valleys, hills, and plains, from 700 to 2200 m, sometimes on calcareous formations, often in dry, exposed places.

Siberia: "Altai," ex Herb. Acad. Petrop. (B, P) m.v. 3; Irkutsk Prov., Irkutsk, among stones, *Turczaninow* in 1829 (DL, Bo, DC in Herb. Prod. vii, 168, n. 36, see pl. 9); Transbaikalia, *Turczaninow* (Bo, P, US, G) m.v. 1, part; Dahur (= Transbaikalia), Nertschinski, on sand hills, *Karo 64* (B, P, Fl, Genoa, Mo). **Manchuria:** Solonia, valley of the Keroulen R., granite knoll, *Chaffanjou 1702* (P). **N. China:** *Licent 5944* (K) m.v. 2; Chili Prov., Hsuan-hua-hsien, Yen-tung-shan, *Anderson 106* (B); Hsiao-wu-tai-shan, Tao-lai-shui, *Smith 148* (Upsala); Peking, middle slopes of the Leong-lin-chan Mts., near the Trappists' monastery, *Bodinier 234* (P); Shansi Prov., Che Sui Hsien, *Ling 9387* (UC). **Mongolia:** Eastern Qurato, calcareous terrain, *David 2667* (B, P); Qurato, high mountain, dry and exposed, *David 2833* (P); Outer Mongolia, Artsa Bogdo, summit meadows, *Chaney 378* (US, NY, G, UC); Outer Mongolia, Tamir R., meadows, *Pavlov 1499* (Mose); Urtu R., *Pavlov* (UC); Heutu R., *Pavlov* (UC); N. Mongolia and Khangai, right bank of Naryn-Khamaryn-gol R., near the crossing to the Tsitgerlik R., *Ikonnikov-Galitsky 617* (NY). **Dzungaria:** Sairam-nor, mountains, *Chaffanjou 976* (P). **Tibet:** Odon-tchalon (Odon-tala ?) Mt., on a hill of the "Zorn-schiffer" near Konde station along way to the mountain, *Patrin* in 1785 (DL).

Although known for more than a century, and widely distributed throughout N.-Central and N.E. Asia, this distinctive species is poorly represented in most collections, and available herbarium specimens are mostly without fruits. Fruits were found, however, on 3 specimens, one from Dzungaria in far W. Mongolia and 2 from N.E. China. Also, through the kindness of Dr. M. Navashin, viable seeds were obtained from the collections of N. Pavlov in Outer Mongolia, and garden cultures grown from these produced abundant fruits. In all this material the achenes display little variation except in degree of attenuateness upward. Floral characters are somewhat variable, especially in size of the parts, but here also, so far as it has been possible to study the necessary details, there is relative constancy. For example, the truncate-crested and hooded ligule teeth shown in fig. 136, c' seem to be typical of this species, as also are the rather long, oblong anther appendages. Striking variability, however, appears in size of plant, particularly in width of rosette or length of leaves and height of stem. The evidence from garden cultures shows that some of these variant forms differ under uniform conditions and must therefore be ecotypes. But many of the extremely reduced forms found among herbarium material are probably ecads, caused by exposure and drouth. An extreme example is found in m.v. 3. Two other forms seem to be sufficiently outstanding to be worthy of special notation.

Minor Variants of *C. crocea*

1. Flower parts small; 4 plants 1.3–1.7 dm high; caudex, leaves, stems, branches, peduncles, and involucre typical; corolla 13.5 mm long; ligule 1.5 mm wide; teeth 0.3–0.5 mm long; corolla tube 4.5 mm long, slender, apparently glabrous but sparsely beset with minute 2-celled acicular hairs; anther tube yellow, 4 × 1 mm dis.; appendages 0.75 mm long, oblong; filaments 0.75 mm longer; style branches 1.5–2 mm long, 0.15 mm wide, attenuate, yellow; achenes lacking; pappus white, 6–7 mm long. *Turczaninow* (G), Transbaikalia, Siberia.

2. Unusually tall; caudex and leaves typical; plant 3.5 dm high; remotely branched from near base upwards, branches, all but lowest one, long, pedunculate; middle cauline leaf shortly petiolate, pinnately parted with linear acuminate lateral segments; peduncle and involucre typical; corolla (immature) 10 mm long; anther tube yellow; achenes lacking; pappus white, 7–8 mm long. *Licent 5944* (K) N. China.

3. (*Hieracium polytrichum* var. *apricum* Bunge, Enum. Alt. 81. *fade* Ledeb.; *H. crocatum* Bunge in herb.; *Crepis Pallastii* var. *pumila* Ledeb., Fl. Ros. 2: 825. 1844–1846.) An extremely reduced form, perhaps an ecotype; but, as Bunge's varietal name implies, the very small size may be largely due to exposure. Whole plant 0.4 dm high; leaves 2 cm long; caudex, leaf shape and indumentum typical; stems scapiform, 1-headed; ligules, style branches and pappus typical. *Bunge* (B ex Herb. Acad. Petrop.), Altai (along the Tschuja R., *fade* Ledeb.). Ledebour also cites specimens from the Baikal and Transbaikalian regions.

Relationship

Crepis crocea is most nearly related to *C. oreades* and *C. Bungei*, which are thought to be its parents (see the synoptical comparison of the 3 species, table 14).

The hypothesis of this hybrid origin of *C. crocea* is supported by the evidence from comparative morphology of the chromosomes. The 16 chromosomes from somatic cells are easily resolvable into 2 groups of 8, each with 4 pairs, which closely resemble the 2 *n*-groups of *C. Bungei* and *C. oreades*, with the exception that 1 pair of satellited chromosomes has lost the satellite. It being possible for such a loss to have occurred in various ways, little if any objection can be raised to this hypothesis.

The geographic distribution of the 3 species is in excellent agreement with the hypothesis of the origin of *C. crocea*. The putative parents are known from closely adjacent regions (see *C. oreades*, p. 502), whereas *C. crocea* covers most of the areas occupied by the 2 parents and has a much wider distribution than either. The fact that the parental species occur in different life zones, *C. oreades* being alpine and high montane and *C. Bungei* occurring at lower altitudes, is not a very serious objection. At present we have comparatively little definite information about the altitudinal limits of natural distribution for the two species; and, even if they are usually well separated in this way, it would be entirely possible for *C. oreades* to appear at lower altitudes occasionally. In this connection the fact that *C. crocea* is known to range from 700 to 2200 m is perhaps significant.

Genetic evidence is limited to data on some F_1 hybrids between *C. Bungei* and *C. crocea*. These hybrids were intermediate between the two species and exhibited a low degree of fertility.

All available evidence, therefore, is in harmony with the hypothesis that *C. crocea* originated through natural hybridization between *C. Bungei* and *C. oreades*, followed by amphidiploidy and the consequent loss of the satellites from one pair of chromosomes.

93. *Crepis tenerrima* (Sch. Bip.) R. E. Fr.

Svensk Bot. Tidskr. 22: 356. 1928 excl. syn. p.p. (Fig. 137.)

Perennial, 2-3 dm high; root woody, elongated; caudex slender, 4-7 mm wide, black-scaly, simple c; shortly 2-3-furcate; caudical leaves up to 15 cm long, 3.5 cm wide, spatulate, blade obovate to oblanceolate, apiculate, denticulate to lyrate pinnately parted with triangular to oblong obtuse lateral lobes, attenuate into a very narrow winged petiole $\frac{1}{3}$ - $\frac{2}{3}$ as long as the blade, \pm pubescent with fine yellow glandless hairs; cauline leaves lance-linear, acute or acuminate, denticulate to pinnately lobed with narrow acute segments, shortly petiolate or sessile, uppermost bractlike; stems several, ascending or semidecumbent, very slender, striate, glabrous or puberulous, remotely 1-2-furcate, 2-3-headed, branches mostly strictly erect, with narrow angles at the forks; peduncles 7-25 cm long, bracteate or with 1 or 2 small leaves, sparsely setulose with black glandless setules and tomentulose near head; heads semierect or half-nodding, medium to large, 25-30-flowered; involucre campanulate, 9-13 mm high, 5-8 mm wide at middle, fuscous-tomentose and setulose with rather long black glandless setules; outer bracts 7-8, unequal, longest $\frac{1}{2}$ as long as inner bracts, linear, 0.5-0.75 mm wide at base, paler than inner bracts, becoming scarious and lax; inner bracts 8-14, in 2 unequal series, outer ones shorter and narrower, inner broadly membranous-margined, lanceolate, obtuse and white ciliate at apex, glabrous on inner face, becoming indurate but not much changed at maturity; receptacle fimbrillate; corolla 14 mm long; ligule 1-1.5 mm wide, with a few tortuous several-celled hairs on outer face; teeth 0.25-5 mm long (in some plants all about 0.25 mm), gland-crested, the crest black in sic.; corolla tube 4.5 mm long, glabrous or with a few hairs near summit; anther tube 2.5×1 mm dis.; appendages 0.75 mm long, oblong, obliquely acute; filaments 0.75 mm longer; style branches 1 mm long, strongly flattened, 0.15 mm wide, acute, green, yellow

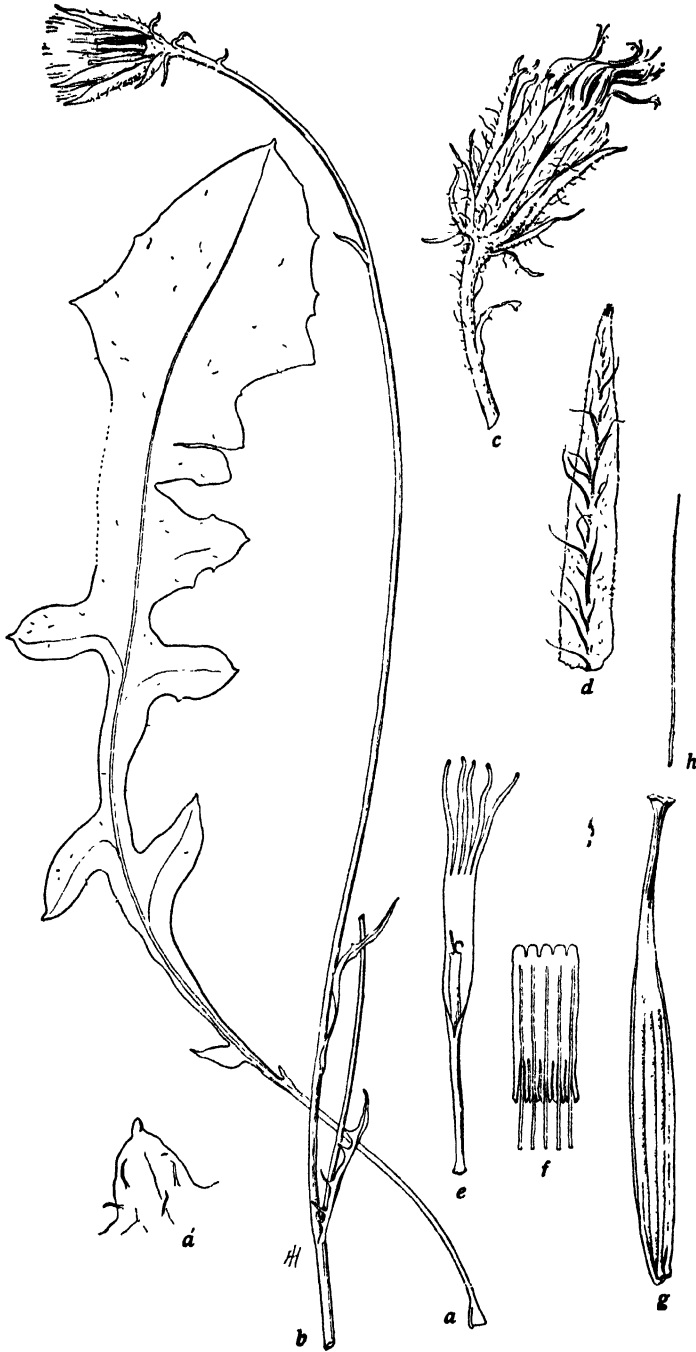


Fig. 137. *Crepis tenerrima*, from type (PC): a, caudical leaf, $\times 1$; a', lateral lobe of young leaf, $\times 4$; b, upper half of 1 branch of flowering stem, $\times 1$; c, head, after anthesis, $\times 2$; d, inner involucre bract, outer face, $\times 4$; e, floret lacking ovary, $\times 4$; f, anther tube, $\times 8$; g, achene, $\times 8$; h, pappus seta, $\times 8$.

on inner face; achenes pale brown, 7–8.5 mm long, 0.75 mm wide, subterete, fusiform, strongly attenuate upward or definitely beaked, 0.2–0.3 mm wide below the slightly expanded pappus disk, constricted at the narrow calloused hollow base, 10-ribbed, ribs nearly equal, rather narrow, rounded, finely spiculate toward the apex; pappus pale tawny, 5.5–6 mm long, 1–2-seriate, setae nearly equal, rather fine, 25–30 μ wide at base, persistent but falling away easily. Flowering Jan.–Feb.; flowers yellow.

Barkhausia tenerrima Sch. Bip., ex Richard, Fl. Abyss. 1: 464. 1847.

Brachyderea tenerrima Sch. Bip., ex Schweinf., Fl. Aethiop. 1: 282. 1867.

Known only from the type locality, which is stated by Richard (*loc. cit.*) to be in Semiène (Simen, Semen) Prov., a mountainous reg. between Amhara and Tigre provinces in N. Abyssinia.

The type is in herb. Cosson (Paris); photograph and fragments in Herb. Univ. Calif.

Monomorphic.

Abyssinia: "In humidis ad rupes in montis Silke," Schimper 677 in 1840 (PC type, P, K, B, UWK).

Noteworthy is the unusual variability in length of the ligule teeth in this species. In the same head and even on a single corolla, the teeth may range from 0.25 to 3–5 mm long. Again, on some plants all the corollas have uniformly short teeth. Apparently this variability has a genetic basis, but it may involve only a single pair of genes.

Relationship

Crepis tenerrima is closest to *C. xylorrhiza*, but is very distinct in the narrow caudex bearing few leaves, the strict branches with narrow angles, the pinnatifid later caudical and early cauline leaves, the nearly glabrous corolla tube, the narrower and more definitely beaked achenes, and especially the nearly equal, rather fine pappus setae. Furthermore, the two species flower at widely different seasons. It is less close to *C. carbonaria* and *C. Ellenbeckii*, even though the long black setae on the involucre and the shape of the achenes are reminiscent of sec. 8. The comparatively large lyrate leaves of *C. tenerrima* also make it appear more primitive than *C. xylorrhiza*, although it is actually less primitive in some features of the involucre, florets, achenes, and pappus.

94. *Crepis xylorrhiza* Sch. Bip.

Mscpt.,¹ with type in herb. Cosson, 6/2, 1854; Schimp. ! it. abyss. sec. V, 1854.

(Pl. 10. Fig. 138.)

Perennial, 0.8–1.4 dm high; root elongated, woody, 0.5–1.5 cm wide, simple or furcate near summit, expanded into a mat-forming caudex 2–7 cm wide, bearing many leaves and several stems; caudical leaves 3–9 cm long, 1–2 cm wide, obovate, obtuse or slightly acute, apiculate, sinuate-denticulate or dentate, strongly attenuate into a narrow winged petiole nearly equal to blade, pubescent on both sides with yellow glandless setiform hairs; cauline leaves lanceolate, acuminate or linear, the lower remotely dentate, teeth mostly narrow, acuminate and sometimes more numerous and crowded at the sessile base, uppermost leaves bractlike but often with one pair of narrow teeth at base; stems erect, slender, glabrescent or sparsely setulose near base, pedunculate or 1–2-furcate and 2–4-headed, the branches spread-

¹ "Ach. 2¼–2¾ lin. longa brunea brevi rostrata in apicem paulo attenuata rostro robusto non distincte ach. bipart. subaeq. pappus 1½ lin. longus sordidus 1 ser. copiosus denticulatus."—C. H. Schultz Bipontinus, notes filed with type.

ing at a wide angle; peduncles 5–12 cm long, sparsely setulose toward head, with short black glandless setules; heads erect, medium, 25–30-flowered; involucre campanulate, 9–10 mm high, 4–6 mm wide at middle, fuscous-tomentose at base, the bracts tomentulose and sparsely setulose with short black glandless setules; outer bracts 10–12, unequal, $\frac{1}{2}$ – $\frac{2}{3}$ as long as the inner, linear, acute, pale brown, black-tipped; inner bracts 10–12, lance-linear, acute, brownish-green, black-tipped; glabrous on inner face, becoming convex dorsally and indurate but not much thickened in fruit; receptacle fimbriate; corolla 11–13 mm long; ligule 1.5 mm wide;

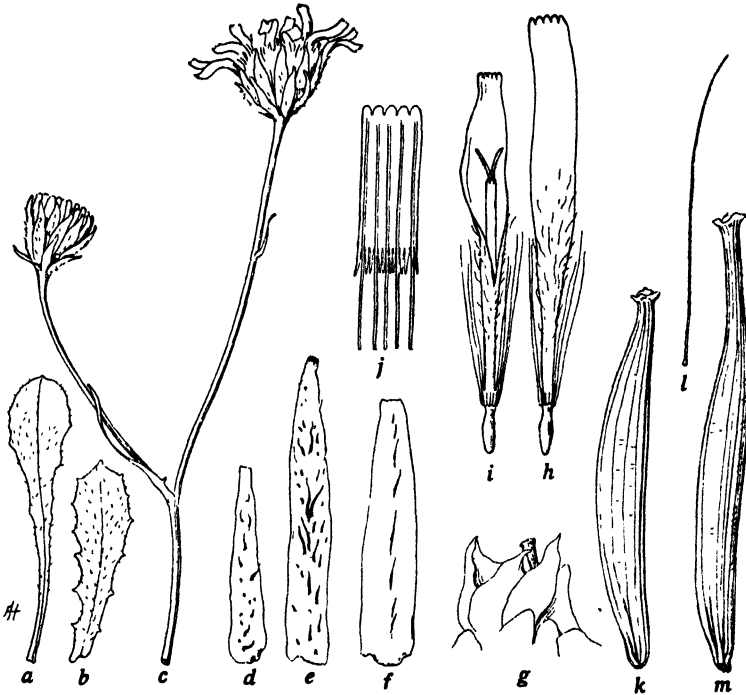


Fig. 138. *Crepis xylorrhiza*, from type (PC), except *b*, *i*–*k*, from Schimper 371 (Bo): *a*, *b*, caudical leaves, $\times 1$; *c*, flower stem, $\times 1$; *d*, outer involucre bract, outer face, $\times 4$; *e*, *f*, inner involucre bracts, outer face, $\times 4$; *g*, detail of receptacle, $\times 25$; *h*, *i*, marginal and inner florets, $\times 4$; *j*, anther tube, $\times 8$; *k*–*m*, marginal and inner achenes and a pappus seta, $\times 8$.

teeth 0.2–0.4 or sometimes to 0.8 mm long, white- or black-crested; corolla tube about 4 mm long, densely pubescent with tortuous several-celled hairs up to 1 mm long; anther tube 2.75 \times 1 mm dis.; appendages 0.5 mm long, acute; filaments 1.25 mm longer; style branches 0.8–1 mm long, 0.1 mm wide, green; achenes medium brown, 6–7 mm long, 0.8–0.9 mm wide, the marginal curved, the inner straight, all fusiform, equally attenuate to both ends, prolonged toward summit into a very short coarse ribbed beak 0.3–0.4 mm wide, with slightly expanded pappus disk, constricted at the lightly calloused hollow base, 10–12-ribbed, ribs nearly equal, rather strong, rounded, strongly spiculate toward summit; pappus tawny, about 5 mm long, 1–2-seriate, setae unequal in width, 25–45 μ wide at base, rather stiff and brittle, persistent. Flowering Aug.; flowers yellow.

Brachyderea xylorrhiza Sch. Bip., ex Schweinf., Fl. Aethiop. 1: 283. 1867; Oliver, Fl. Trop. Afr. 3: 448. 1877.

The type is in herb. Cosson, Paris; photographs and fragments in Herb. Univ. Calif.

N. Abyssinia, in the Simen Mts., 2800–3600 m alt., in moist places.
Monomorphic.

Abyssinia: Amhara-Tigre Prov., Simen Mts., Mt. Boahit (= Buahit), Acallo Meda, alpine, *Schimper* 371, Aug. 17, 1852 (P), as *B. tenerrima* Sch. Bip.; without definite locality, *Schimper* 371, June 2, 1854 (PC ex herb. Sch. Bip.) type; Simen, "371. collectione ani 1852" (Stockholm); without definite locality, *Schimper* 371 (Bo); Mt. Boahit and Debr. Eski, 2817 m, *Schimper* 33B (P).

Relationship

Although the label with the type bears Schultz's note, "aff. *C. abyssinica*," yet *C. xylorrhiza* is much closer to *C. tenerrima*. From the latter, however, it is very distinct in the expanded, mat-forming caudex, the broad angles between stem and branches, and the merely denticulate cauline leaves, as well as the densely pubescent corolla tube, the less definitely beaked achenes, and especially in the unequal width of the pappus setae.

95. *Crepis Hookeriana* J. Ball.

Jour. Bot. 11: 371. 1873; Jour. Linn. Soc. 16: 538. 1878; non Clarke, 1876, nec Oliv. et Hiern., 1877. (Fig. 139.)

Perennial, 0.5–1.5 dm high; caudex woody, densely covered with brown bases of old leaves, 0.5–2 cm wide, 1–6 cm long, simple or 2–4-divided, attenuate into a long straight woody taproot, leafy at crown; leaves all caudical, 2–9 cm long, 0.5–2 cm wide, oblanceolate, acute or obtuse, deeply pinnatifid to pinnately parted, terminal lobe triangular to elliptic or rotund with truncate base, lateral lobes triangular to lance-linear, acute or acuminate, petiole short or equal to blade, narrowly winged, broader at base, pubescent on both sides with or without glands, or glabrescent with scattered floccules of white tomentum; stems sinuate, scapiform, always 1-headed, with several small linear bracts, slender, white-floccose or glabrescent; heads erect, medium, 30–40-flowered; involucre campanulate, 10–11 mm high, 5–6 mm wide at middle in fruit, dark green, white-floccose, \pm setose with short or a few longer black setae with or without brown glands; outer bracts 8–12, unequal, longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner, linear, appressed; inner bracts 13–18, lanceolate, acute, white-ciliate at apex, glabrous on inner face or with a few short white trichomes, slightly carinate but scarcely changed dorsally in fruit; receptacle alveolate, fimbriellae very shortly ciliate; corolla about 12 mm long; ligule 1.3 mm wide, sparsely beset on lower $\frac{2}{3}$ with short white trichomes; teeth 0.5 mm long; corolla tube 4 mm long, shortly pubescent; anther tube about 5×1 mm dis.; appendages 0.8 mm long, oblong, sagittate; filaments 0.5 mm longer; style branches 2.25 mm long, slender, yellow; achenes brown, 5.5–6.5 mm long, 0.6–0.7 mm wide, fusiform, equally attenuate to both ends, with slightly expanded pappus disk, thinly calloused at the very small base, 16–18-ribbed, ribs rounded, unequal, with a notable tendency for alternate ribs to be stronger, spiculate toward the apex; pappus white, 5–6 mm long, 2-seriate, setae about equally fine, coarsest $40\text{--}50\mu$ (5 cells) wide at base, firm but pliable, persistent. Flowering May–July; flowers yellow, outer face of ligules reddish-purple. Chromosomes, $2n = 8$.

Hieraciodes Hookerianum O. Kuntze, 1: 346. 1891.

Crepis Sibthorpiana subsp. *Hookeriana* (Ball) Pau et F. Q., in herb. Font Quer, Iter. Marocanum, 1920, n. 480.

Morocco, Great Atlas and rarely in lesser ranges; siliceous and calcareous rocks and deposits, 2300–3500 m alt.

Monomorphic.

Morocco: W. part, peak of Djebel Teza, *J. Ball* in 1871 (K, type and isotype, UCf); Great Atlas, Amsmiz Valley, *J. Ball* in 1871 (CP); Great Atlas, *J. Ball* (Fl); Great Atlas, *Hooker* in

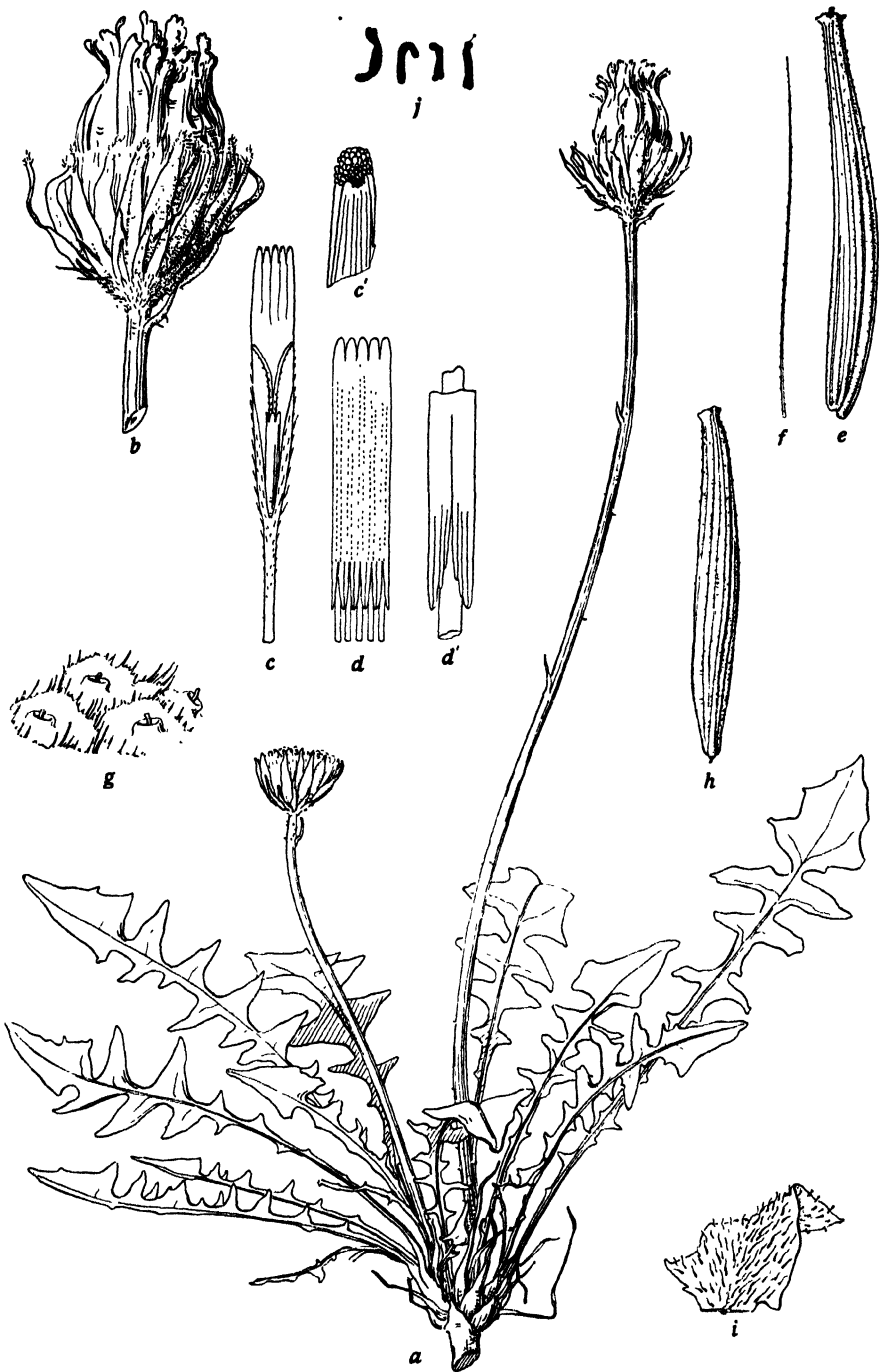


Fig. 139. *Crepis Hookeriana*, a-f, from type and isotype (K); g-j, from hort. genet. Calif. 1458 (Maire in 1922, UC 296070): a, plant, $\times 1$; b, head, $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule tooth, $\times 25$; d, anther tube, $\times 8$; d', detail of appendages, $\times 32$; e, f, achene and pappus seta, $\times 8$; g, detail of receptacle, $\times 25$; h, achene, $\times 8$; i, tip of leaf showing pubescence, $\times 2$; j, somatic chromosomes, $n = 4$, $\times 1250$.

1871 (K); *ibid.*, Tumminen Valley, *Jahandiez* in 1921 (Ms); *ibid.*, Djebel Ouensa, southwest of Morocco, *Ibrahim* in 1875 (K, Ms); *ibid.*, Prov. Demnat, Djebel Rat, *Ibrahim* in 1879 (K); *ibid.*, Reraya, Tizi-n-Tagherat, 3500 m, *Maire* in 1922 (UC); Er Rif (?) summit of Mt. Tidighin (Tidighin), 2400 m, *Font Quer* in 1929 (UC), as *C. Sibthorpiana* subsp. *Hookeriana*.

Relationship

Crepis Hookeriana, with its sometimes suffruticulose caudex and unequally ribbed achenes, must be considered a fairly primitive species. Its scapiform stems and deeply penetrating taproot certainly place it in this section. From the reduction in size of heads, flowers, and fruits, it is a more advanced species than *C. Schachtii* or *C. oreades*.

96. *Crepis Faureliana* Maire

Bull. Soc. d'Hist. Nat. Afr. Nord. 29: 426. 1938. (Fig. 140.)

Perennial, 0.4–1 dm high; caudex woody, 1 cm long, 1–1.5 cm wide, covered with brown bases of old leaves, constricted at base into the vertical woody taproot, simple or divided, leafy at crown; leaves all caudical, 2–4 cm long, 0.3–0.6 cm wide, oblanceolate, acute or obtuse, denticulate or runcinate-dentate to subpinnatifid, the teeth or small lateral lobes salient, attenuate into a winged petiole, broader at base, densely pubescent with fine short gland hairs; stems 1 per caudex, scapiform, 1-headed, slender, arcuate, leafless or 1–2-bracteate, finely gland-pubescent and near the head densely white-tomentose; heads erect, small, 35–40-flowered; involucre cylindric-campanulate, 10–11 mm long, 4–5 mm wide at middle in fruit, canescent tomentulose, pubescent with fine short pale or black gland hairs; outer bracts about 10, all from $\frac{1}{2}$ to $\frac{2}{3}$ as long as the inner, linear, brownish at the acute apex; inner bracts about 13, lanceolate, acute, white-ciliate at apex, glabrous on inner face, becoming strongly convex and indurate in mature fruiting heads, ultimately half-reflexed; receptacle alveolate, alveolae deep, 0.3–0.4 mm wide, fimbriae membranous, densely white-ciliate at margin, cilia mostly about 0.3 mm long, with an occasional one about 1 mm long; corolla 10.5–12.5 mm long; ligule 2–3 mm wide; teeth 0.2–0.5 mm long; corolla tube 2.5–3.3 mm long, pubescent with stiff acicular hairs 0.1–0.15 mm long; anther tube 4.75×1.25 mm dis.; appendages 0.5 mm long, oblong, obtuse; filaments 0.5 mm longer; style branches 2.5 mm long, 0.1 mm wide, yellow; achenes light brownish-yellow, 4.5–5 mm long, 0.6 mm wide, fusiform, strongly attenuate near summit, 0.2–0.3 mm wide below the expanded pale pappus disk, constricted at the oblique pale-calloused hollow base, 10-ribbed, sometimes with faint traces of additional ones, ribs about equal, narrow, round, finely spiculate from base to apex; pappus white, 5–6 mm long, 2–3-seriate, setae nearly equally fine, the coarsest 20–25 μ (3–4 cells) wide at base, rather rigid but pliable, persistent. Flowering June; flowers yellow, deep purple on outer face of ligules.

Known only from the type locality.

Monomorphic.

E. Algeria: Sahara Atlas Range, Aures Mts., Ras Faraoun, calcareous rocks above "Coup de pied du Pharaon," 1900 m, *Faurel*, July 7, 1937, with fruits, *Maire*, June 23, 1938, with flowers (Alger, UC 620576) type and isotypes.

Relationship

Crepis Faureliana is an especially interesting species because of its obvious close relationship to *C. Hookeriana* and its resemblance to *C. Robertioides* (as pointed out by Maire, *loc. cit.*) as well as to other members of this section. This species is

apparently well isolated from *C. Hookeriana*, which has not been reported from the Sahara Atlas and which occurs at higher elevations in the Great Atlas. The lower elevation and drier climate of the Sahara Atlas coincides with the fact that *C. Faureliana* is greatly reduced in size of plant and its parts.

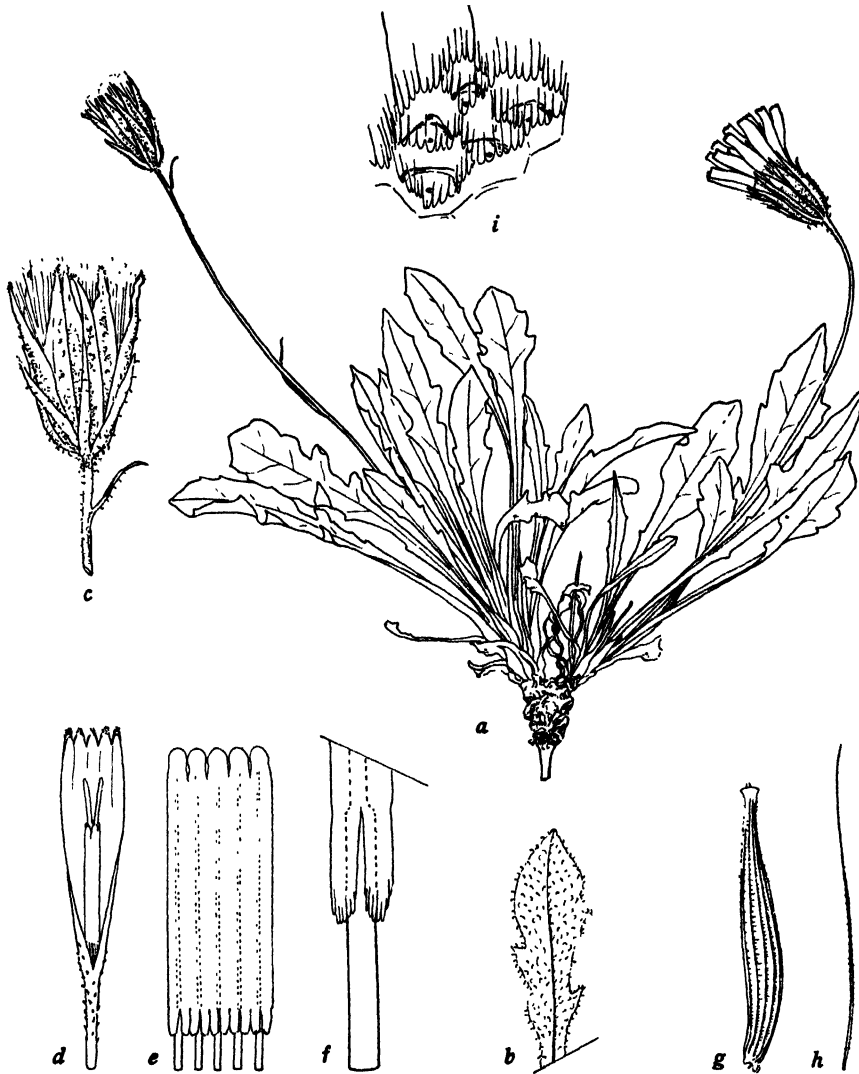


Fig. 140. *Crepis Faureliana*, a-f, and i, from isotypes (UC 620576); g, h, from type (Alger): a, plant, $\times 1$; b, apical part of a leaf, $\times 2$; c, immature head, $\times 2$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, h, achene and pappus seta, $\times 8$; i, detail of receptacle, $\times 25$.

97. *Crepis Robertioides* Boiss.

Diag. Pl. Or. Nov. ser. 1, 11: 59. 1849. (Fig. 141.)

Perennial, forming dense leafy mats 0.5–1 dm wide, and producing slender scapiform stems 0.4–1.4 dm high; caudex stout, woody, in younger plants short, simple, about 1 cm wide at the leafy crown, in older plants \pm divided and then up to 3 cm wide, sometimes elongated and with subterranean branches, attenuate into a strong vertical taproot, often bearing strong woody fibers; leaves all caudal,

3–7 cm long, 0.3–1 cm wide, linear to oblanceolate, obtuse or acute, dentate or pinnatifid with triangular teeth or lobes, or pinnately parted with triangular oblong or linear entire or dentate lobes, rachis narrow, petiole short, narrowly winged, scarious at the much broader base, glabrous or canescent-tomentulose or rarely pubescent with short pale glandless hairs; stems simple, 1-headed, or divaricately 2–4-branched very near the base, the branches or stems erect or arcuate, terete, few-bracteate, slightly thickened near head in fruit, glabrous, tomentulose or finely gland-pubescent above; heads erect, small, 11–19-flowered; involucre cylindric-campanulate, 9–10 mm long, 4–5 mm wide at middle in fruit, canescent-tomentulose, sometimes sparsely beset with short black setules, rarely gland-pubescent; outer bracts 5–7, unequal, longest about $\frac{1}{3}$ as long as the inner, lance-linear, acute or acuminate; inner bracts 8–10, lanceolate, acute, broadly membranous-margined, apparently glabrous on inner face, but under lens usually with a few shining trichomes, becoming convex-carinate dorsally and prominently spongy-thickened near base at full maturity; receptacle areolate-fimbrillate, fimbrillae low, very shortly white-ciliate; corolla 14–15 mm long; ligule 2.5–3 mm wide; teeth 0.3–0.6 mm long; corolla tube 5 mm long, pubescent above the middle with salient acicular hairs 0.1–0.8 mm long; anther tube 4.3×1.5 mm dis.; appendages 0.6 mm long, oblong, truncate; filaments 0.7 mm longer; style branches about 3 mm long, 0.2 mm wide, yellow; ovary obconical, truncate at summit, with a border of white cilia definitely *below* the pappus disk, cilia 0.25–0.5 mm long, persisting and present on the mature achenes, sometimes appearing like a crown of short pappus; achenes stramineous or light brown, 5–5.5 mm long, fertile ones 1.3–1.6 mm wide, subterete or subcompressed, fusiform, abruptly attenuate at both ends, 0.5–0.6 mm wide just below the slightly expanded pappus disk, strongly constricted at the small thinly calloused base, 20-ribbed, the ribs nearly equal but with a definite tendency for every fifth rib to be stronger, especially in the marginal achenes, all the ribs rather narrow, rounded, smooth, with a narrow zone of white cilia just below the pappus disk and occasionally with scattered cilia more than 1 mm below the pappus disk; pappus nearly white, slightly yellowish, 6–7 mm long, 3–4-seriate, the setae unequal, 30–65 μ wide at base, rather soft but persistent. Flowering July–Sept.; flowers yellow, reddish-purple on outer face of ligules. Chromosomes, $2n = 8$.

Derouetia Robertioides Boiss., *Diag. Pl. Or. Nov. ser. 2*, 5: 115, 1856.

Hieraciodes Robertioides O. Kuntze, *Gen. 1*: 346, 1891.

S.W. Syria in mountains of Anti-Liban and Liban at elevations ranging from 1750 to 2890 m; subalpine and alpine.

The type is in herb. Boiss.; it is the middle one of the three plants first cited below (cf. photograph in Herb. Univ. Calif.).

Monomorphic.

Syria: Anti-Liban, Mt. Hermon, summit, *Boissier* in July, 1846 (Bo) type; Mt. Hermon reg., near melting snow, *Kotschy 177* (Bo); Mt. Hermon, 2500–2600 m, *Eig* in 1924 (HU); Djebel Scheik, Mt. Cheba (Hermon, *fide* Boiss.), *Gaillardet* in 1816 (Bo, UCf) as *Derouetia Robertioides*; Liban, Orin, Karn, Yamouny, etc., *Blampton* in 1855 (Bo, UCf); Hassoun, *Boissier* in 1859 (Bo), as *Derouetia Robertioides*; Liban, summit, *Hooker and Hanburg* in 1860 (K); N. Liban, Djebel Makmal and Dj. el Ars, 2600–2900 m, *Bornmüller 12081* (B); Mt. Sanin, peak, *Bornmüller 973* (B); N. Liban, above the forest of Ehden, near Talieh, 1750–1850 m, *Eig and Zohary* in 1931 (UC); mountain ranges between the forest of Ehden and Talieh, 2050–2100 m, *Eig and Zohary* in 1931 (UC); mountain ranges between Ehden and Korneth es Souda, *Tragacanthia* Baths, 2100–2500 m, *Eig and Zohary* in 1931 (UC); mountains near Korneth es Souda, among rocks, 2500–2560 m, *Eig and Zohary* in 1931 (UC); Korneth es Souda, border of snow fields, 2890 m, *Eig and Zohary* in 1931 (UC).

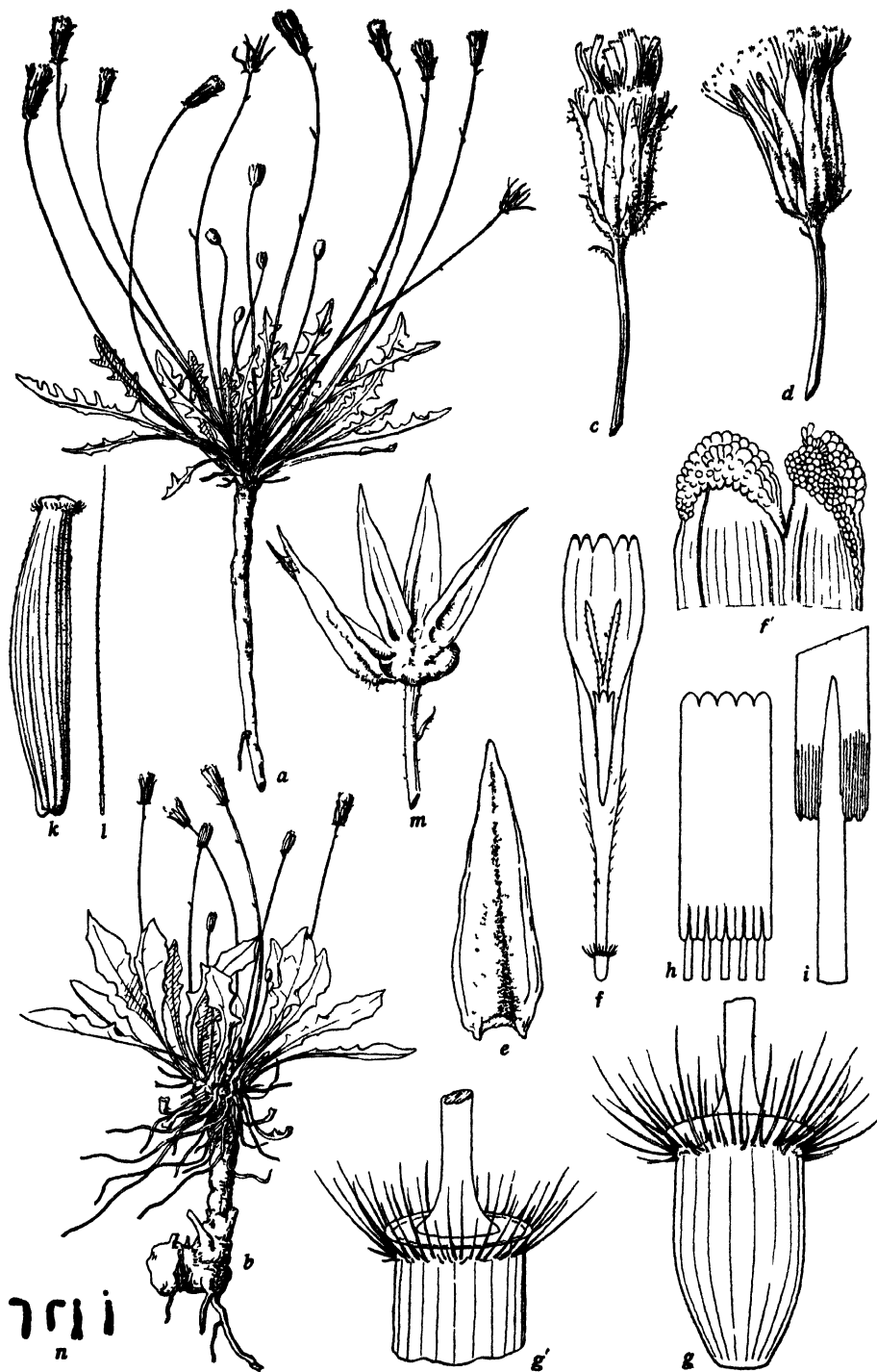


Fig. 141. *Crepis Robertioides*, from Eig and Zohary in 1931 (UC 466641, 466645): a, b, plants, $\times \frac{1}{2}$; c, flowering head, $\times 2$; d, fruiting head, $\times 2$; e, inner involucre bract, outer face, $\times 4$; f, floret including ovary, but omitting pappus, $\times 4$; f', detail of ligule teeth, $\times 25$; g, g', ovary, with pappus omitted, showing subapical cilia, $\times 32$; h, anther tube, $\times 8$; i, detail of appendages, $\times 32$; k, l, achene and pappus seta, $\times 8$; m, old head showing receptacle, $\times 2$; n, somatic chromosomes from hort. genet. Calif. 3129 (grown from seeds collected by Eig and Zohary in Liban, Korneth es Souda, border of snow fields, Sept. 3, 1931; cf. UC 466642), $n = 4$, $\times 1250$.

Relationship

Crepis Robertioides has no very close relatives; but it exhibits strong resemblances to several species in this section; for example, to *C. oreades* in its sturdy divided caudex, numerous small pinnatifid leaves, and scapiform stems; to *C. crocea* in its rather short and broad, 20-striate achenes and 3-4-seriate pappus. But its much smaller flower heads and small number of florets per head make it a more reduced species than any of the preceding ones.

The occurrence of subapical cilia on the achenes is very rare in this genus. They occur in *C. alpestris*, *C. alpina*, and *C. syriaca*, but seldom so prominently developed. They are reminiscent of the short outer crown of true pappus found in certain species of *Lactuca* subg. *Mulgedium*. But these cilia are not pappus setae; they are simply hairs, or several-celled trichomes which are 1 cell in width borne on the epidermis of the achene just below the summit. Although the achenes in *C. Robertioides* are often subcompressed, and in the marginal achenes 2 of the stronger ribs are often marginal, the other achenes are subterete and have no "marginal" ribs. Such achenial characters as those just described are frequently found in the more primitive species of *Crepis*. Furthermore, the habit, leaf shape, involucre, flower color and pappus of *C. Robertioides* are all characteristic of *Crepis*.

98. *Crepis heterotricha* DC.

Prod. 7: 186, 1838. (Figs. 142, 143.)

Perennial, 0.4-1.8 dm high; root woody, vertical, 3-5 mm wide; caudex 0.3-5 cm long, 0.5-2 cm wide, simple or several times divided and forming a compact conical or globose leafy mass; caudical leaves small, oblanceolate, dentate to sub-pinnatifid or deeply pinnatifid, petiolate, the petiole conspicuously broadened, stramineous and spongy-thickened at base, \pm hispid with short yellow glandless hairs; cauline leaves absent or represented by 1 or 2 small bracts; scapes 1-4, slender, erect or flexuous, terete, striate, hispidulous, not fistulose, not enlarged at base of the fruiting head; heads erect, small to medium, 15-20-flowered; involucre campanulate, 10-14 mm long, about 5 mm wide at middle, dark green with broad yellow margins on all the bracts, usually hispid with yellow glandless setules, especially at the base, and \pm gland-pubescent with very short yellow hairs scattered among the much longer setules, but sometimes lacking the setules and merely gland-pubescent; outer bracts 6-10 or 12-18 in the two subspecies, imbricate, very unequal, longest $\frac{1}{4}$ - $\frac{1}{2}$ as long as inner ones; inner bracts 10-12, lanceolate, acute or acuminate, the apex purple in flowering or fruiting heads, ventrally glabrous and strongly nerved, becoming dorsally carinate and spongy-thickened at base in fruit; receptacle not paleaceous; corolla 13-17 mm long, the inner ones sometimes much smaller; ligule 2-2.5 mm wide, yellow, suffused with reddish-purple, pubescent near base with coarse several-celled hairs 0.5-1 mm long; teeth 0.25-1 mm long, conspicuously gland-crested or glandular on upper half of outer face; corolla tube 4.5-6 mm long, pubescent on upper half or near summit like base of ligule; anther tube (4)5 \times 1.25 mm dis.; appendages 0.6-0.75 mm long, acute, united; filaments about 0.75 or 1.75 mm long in the two subspecies; style branches 2.5-3 mm long (1.5 mm in one subspecies), broader at the tip, truncate or acute, yellow; achenes (nearly mature) dark greenish-brown, 6 mm long, 0.5 mm wide, columnar, \pm attenuate to both ends, with slightly broader pale pappus disk and yellow-calloused base, 18-20-ribbed, ribs narrow, finely scabridulous under lens; pappus white, copious, 6-8 mm long, 3-seriate, united at base, the setae very unequal in length and width, 2-8 cells wide at base, soft, persistent. Flowering July.

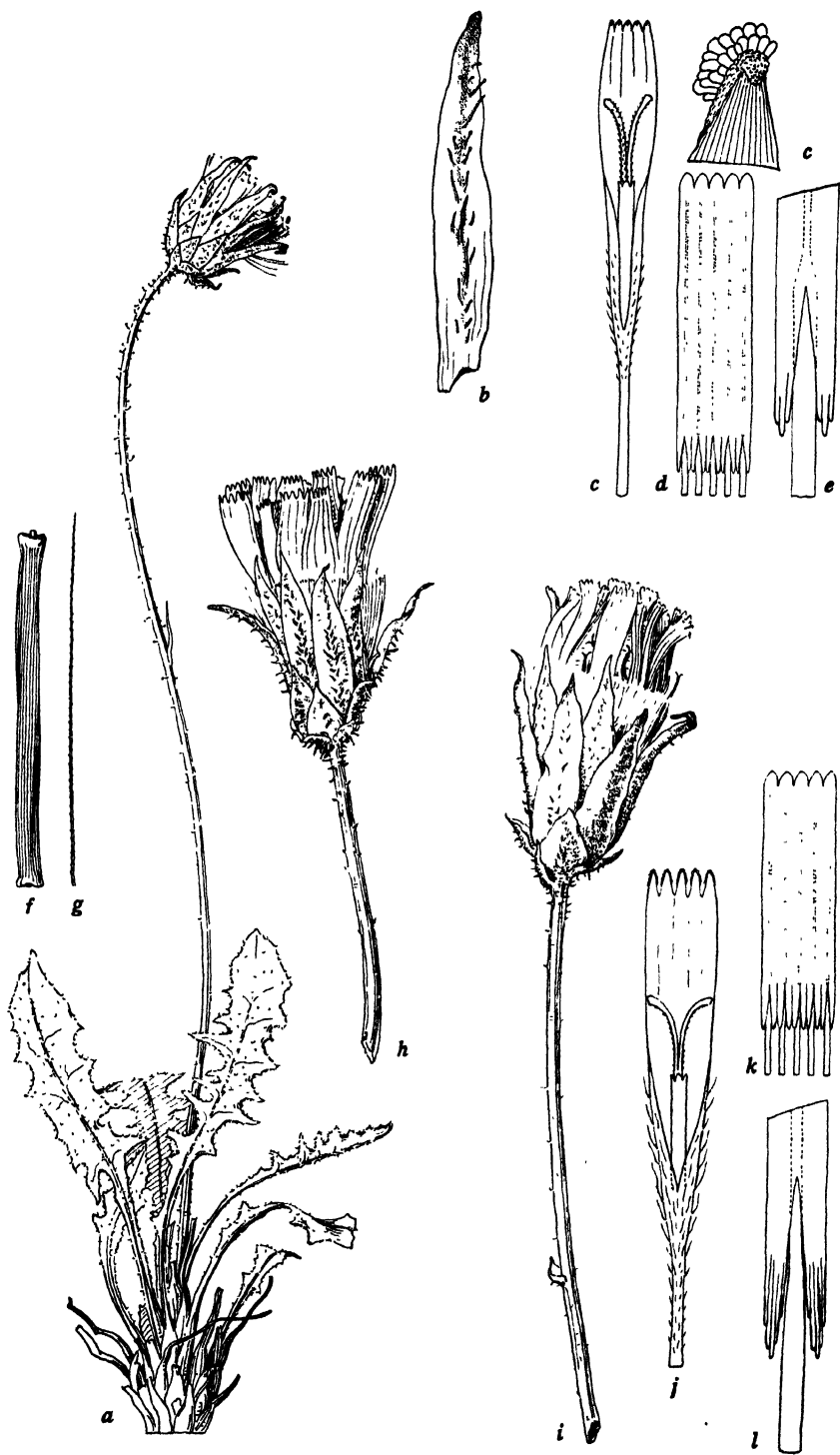


Fig. 142. *Crepis heterotricha typica*, a-g, from type and isotype (DC, K); h, from Kotschy 800 (Bo); i-l, from Bornmüller 5159 (UC 575082): a, plant, $\times 1$; b, inner involucre bract, outer face, $\times 4$; c, floret lacking ovary, $\times 4$; c', detail of ligule tooth, $\times 50$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, g, immature achene and a pappus seta, $\times 8$; h, i, flowering heads, $\times 2$; j, floret lacking ovary, $\times 4$; k, anther tube, $\times 8$; l, detail of appendages, $\times 32$.

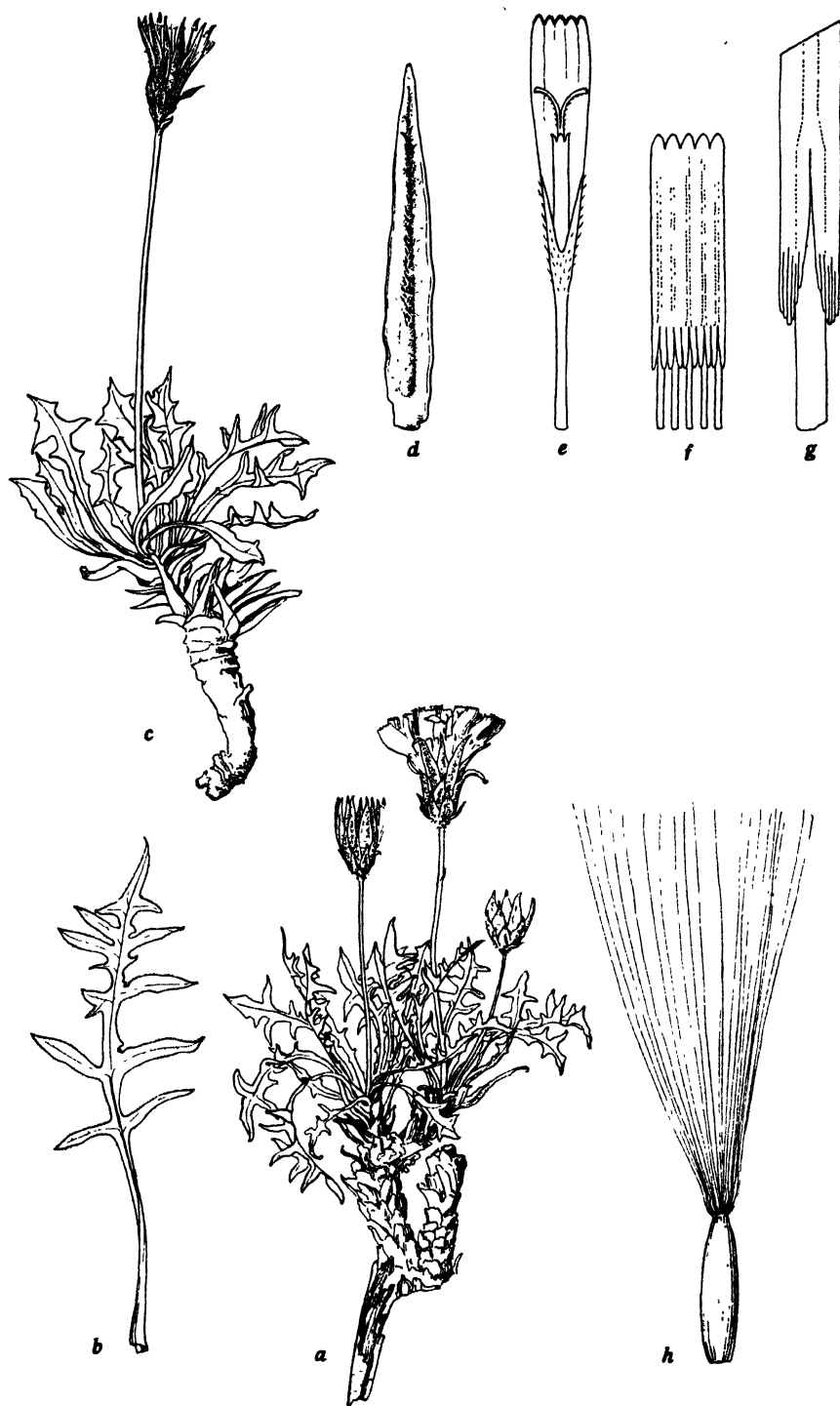


Fig. 143. *Crepis heterotricha lobata*, from type and isotypes (B, UC 575081): a, plant with young heads, $\times 1$; b, leaf, $\times 1$; c, plant with young fruiting head, $\times 1$; d, inner involucre bract from same, $\times 4$; e, floret lacking ovary, $\times 4$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, immature achene and pappus, $\times 8$.

Persia, in high mountains.

This little-known species, represented by only a few herbarium collections, is evidently polymorphic. Although the identity of the type locality is dubious, all the other collections which resemble the type are from southern provinces. De Candolle's spelling of the type locality, "Alpes Zerokou," is an obvious error, since the original label reads Alp. Zerd., and Boissier gives Zerdkuh, which may signify Zardeh Kuh Mts. in S. Khunsar Prov., 120 km northwest of Chigha Khur. It appears, therefore, that all the typical and closely similar forms thus far known occur in S. Persia, whereas Bornmüller's collection of a distinct subspecies is from the Elburz Mts., in the north.

Key to the Subspecies of Crepis heterotricha

- Leaves dentate to subpinnatifid, with broad terminal and relatively short lateral segments, the rachis and petiole broader; outer involucrel bracts 6–10, mostly ovate-triangular, acute 98, *a. typica*
- Leaves pinnately parted, with narrow terminal and relatively long lateral segments, the rachis and petiole very narrow; outer involucrel bracts 12–18, ovate, acuminate 98, *b. lobata*

98, *a. Crepis heterotricha typica* subsp. nov. Folia caudicalia 2–7 cm longa 1 cm lata dentata; scapi plerumque 8–14 cm longi; squamae involucri exteriores 6–10 ovatae acutae; corolla 13–17 mm longa; antherae 4–5 mm longae; rami styli 2.5–3 mm longi; achaenia 6 mm longa; pappus albus copiosus 6–8 mm longus 3-seriatus.

Caudical leaves 2–7 cm long, 1 cm wide, usually with a few remote short very narrow teeth or shallow lateral lobes; scapes 2–16 (mostly 8–14) cm long; outer involucrel bracts 6–10, mostly ovate-triangular, acute; corolla 13–17 mm long; ligules in marginal florets 2–2.5 mm wide, the teeth 0.3–1 mm long; anther tube 4.25–5 mm long, the filaments extending beyond the appendages 0.75 mm; style branches 2.5–3 mm long; achenes and pappus typical. See fig. 142.

Crepis Kotschyana Boiss., Fl. Or. 3: 839. 1875 in syn., non C. B. Clarke.

Hieraciodes heterotrichum O. Kuntze, Gen. 1: 346. 1891.

Persia: Khunsar (†) Prov., Zerdkuh (= Zardeh Kuh †) Mts., *Aucher-Eloy 3549* (DC type, UCf, K); S. Persia, Kuh Da'na Mts., *Kotschy 800* (Bo, B), as *C. Kotschyana* Boiss.; *ibid.*, Bachtari Mts., Mt. Sebsekuh, calcareous rocks, *Haussknecht* in 1868 (Bo); *ibid.*, without locality, *Kotschy 977* (Bo); *ibid.*, Kerman Prov., Mt. Kuh-i-Lalesar, highest peaks, 3800–4000 m, *Bornmüller 5139* (Weimar, B, UC) m.v. 1.

Minor Variant of C. heterotricha typica

1. Florets larger than in typical forms, with longer ligule teeth and more strongly pubescent tube and ligule; corolla 16–17 mm long; ligule 2–2.25 mm wide; teeth 0.75–1 mm long; style branches 2.5 mm long, gradually increasing in width to the truncate tip, which is 0.2–0.25 mm wide; achenes not seen. Upon examination of the pollen some 4-pored grains were seen, which suggests that this may be a polyploid of some sort. However, the pollen in a typical plant (*Kotschy 977*), as well as in subsp. *lobata*, was found to be irregular in size, ranging from 23 to 34 μ and 26 to 36 μ , respectively, and in both plants some large grains, suspected of being 4-pored, were seen. Hence, this species may consist of a series of polyploid forms, this one being merely an extreme variant. *Bornmüller 5139* (B, Weimar, UC) Kuh-i-Lalesar, 3800–4000 m, Kerman Prov., S. Persia.

98, *b. Crepis heterotricha lobata* subsp. nov. Folia caudicalia 2–4.6 cm longa 1–2 cm lata pinnatipartita, segmenti terminali brevi tenui, segmentibus lateralibus 8–12 tenuibus interdum 1-dentatis; scapi 4–6 cm longi ad summitatem interdum tomentosi; squamae involucri exteriores 12–18 ovatae acuminatae; corolla circa 14 mm longa, ligula interdum 2 mm lata; antherae 4 mm longae; rami styli 1.5 mm longi; achaenia (immatura) 3 mm longa virescentia columnaria ad apicem paululum attenuata; pappus albus copiosus 6–8 mm longus 3-seriatus, setis inaequalibus mollibus persistentibus.

Caudical leaves 2-4, 6 cm long, 1-2 cm wide, pinnately parted, with 4-6 pairs of rather close narrow lateral segments and short narrow terminal segment, lateral segments sometimes 1-dentate on lower margin near base; scapes 4-6 cm long, sometimes canescent-tomentose at summit; outer involucre bracts 12-18, ovate, acuminate; corolla about 14 mm long; ligules in marginal florets 2 mm wide, the teeth 0.25 mm long; anther tube 4 mm long, the filaments extending beyond appendages 1.75 mm; style branches 1.5 mm long; achenes (immature) 3 mm long, greenish, columnar, slightly attenuate at summit; pappus white, copious, 7-8 mm long, 3-seriate, united at base, the setae very unequal in length and width, 2-8 cells wide at base, soft, persistent. See fig. 143.

N. Persia: Elburz Mts., Mt. Totschal, alpine peaks, 3800 m, Bornmüller 7536b (B type, Weimar, UC).

Relationship

Crepis heterotricha is nearest to *C. armena*, from which it is very distinct in the broad yellow margins of the involucre bracts, the nonglandular setae of the leaves, the fewer but larger florets, and the truncate style branches. It is certainly less close to *C. bithynica* and *C. Robertioides*. Through the coincidence that the type of subsp. *lobata* was collected on the same mountain as one of Kotschy's collections of *Crepis elbrusensis* (see p. 626), the two were at first confused, but the resemblance is superficial and the receptacle is devoid of paleae in all forms of *C. heterotricha*.

99. *Crepis armena* DC.

Prod. 7: 168. 1838. (Figs. 144, 145.)

Perennial, 0.8-1.5(3) dm high; caudex 5-8 mm wide in old plants, prolonged into a strong, woody taproot, with several strong fibers from near crown, crown simple or 1-divided, covered with brown bases of old leaves; leaves all caudal, up to 7 cm long, 1.9 cm wide, oblanceolate or lanceolate, obtuse or acute, attenuate into a short narrowly winged petiole with broader clasping base, remotely denticulate, later leaves sometimes pinnately dentate with narrow acuminate teeth, densely hispidulous with pale glandular setae; stems 1 or 2 from a caudex, scapiform or occasionally 1-furcate, slender, striate, pubescent near base and near head, bearing 1 or 2 small bracts; heads erect in flower and fruit, medium, 25-35-flowered; involucre campanulate; outer bracts 10-15, unequal, $\frac{1}{3}$ - $\frac{1}{2}$ as long as inner ones; inner bracts 14-18, lanceolate, acuminate, dorsally pubescent, ventrally glabrous; receptacle naked; pappus (4)5-6(7) mm long, white tinged with yellow, soft, rather fine, 3-seriate, persistent, coming away in small clumps.

Asia Minor, E. Anatolia and Armenia.

Although this little-known species is represented by only very scanty herbarium material, critical study of the available specimens reveals the existence of several forms, two of which must be recognized as subspecies and may eventually be found to be true species. On account of the paucity of material, however, it is sufficient for the present to treat them as subspecies.

Key to the Subspecies of *Crepis armena*

- Outer involucre bracts about 10, ovate, obtuse, less than $\frac{1}{2}$ the length of inner ones; inner bracts about 10 mm long; pappus 4-5 mm long 99, *a. typica*
 Outer involucre bracts 10-15, ovate to lanceolate, acute, longest $\frac{1}{2}$ as long as inner ones; inner bracts 12-18 mm long; pappus 5-7 mm long 99, *b. longibractea*

99, *a. Crepis armena typica* subsp. nov. Planta 0.8-3 dm alta; caudex ligneus foliosus; folia omnia caudicalia dense glanduloso-hispidulosa; caules semper (!) scapiformes; involucre 11 mm longum, squamis exterioribus 10 aequalibus ovatis,

interioribus 15 lanceolatis breve acuminatis; achaenia (immatura) viridula 1.5 mm longa; pappus 4–5 mm longus flavo-albus 3-seriatus persistens.

Leaves densely and minutely hispidulous, with very short (up to 0.2 mm long) white stout setae bearing small brown glands; stems always (?) scapiform, fistulose (?), gland-pubescent but not long-hairy near head; involucre 11 mm long; outer bracts 10, ovate, obtuse, nearly equal, longest less than $\frac{1}{2}$ as long as inner ones, irregularly ciliate on margin and, like inner bracts, minutely and densely gland-

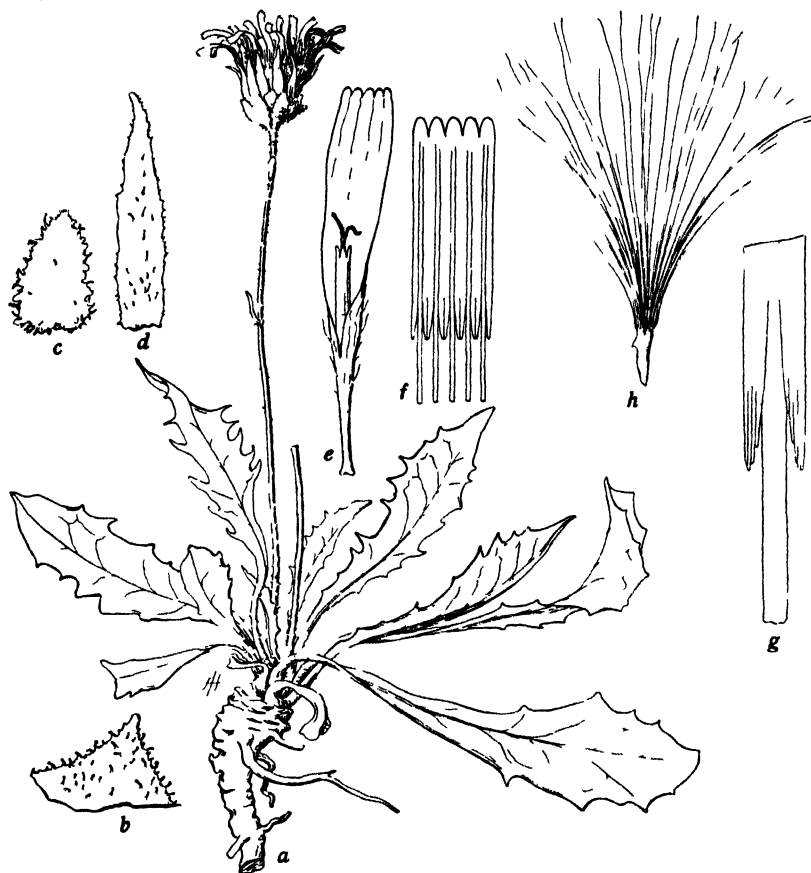


Fig. 144. *Crepis armena typica*, from type (DC). a, plant, $\times 1$; b, lateral tooth and adjacent area of a leaf showing glandulose setae, $\times 8$; c, d, outer and inner involucre bracts, outer face, $\times 4$; e, floret lacking ovary, $\times 4$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, apex of a young achene with pappus, $\times 8$.

pubescent; inner bracts 15, lanceolate, shortly acuminate; corolla 12 mm long, ligule 15 mm wide; corolla tube 4 mm long, pubescent with short acicular hairs; anther tube 3.75×1.25 mm dis; appendages 0.6 mm long, narrowly triangular, acute; filaments 0.6 mm longer; style branches 1.5 mm long, 0.15 mm wide, yellow, achenes (immature) 1.5 mm long, greenish, striate, attenuate toward summit; pappus 4–5 mm long, white tinged yellow near base. Flowering summer ?; flowers yellow. See fig. 144.

Hieraciodes armenum O. Kuntze, Gen. 1: 345. 1891.

Armenia and E. Anatolia, mountains.

In addition to the type material, Aucher-Eloy no. 3280 in 1837, one other specimen (cited below) has been seen by the author, who, at the time, thought it was this

species; but on account of its stature and lack of detailed observations it is now provisionally listed as m.v. 1.

Asia Minor: Armenia (Ilirae ? or Thezae ?), *Aucher-Eloy 3280* (DC type, Bo, UCf, P); Armenia turcica, *Sintenis 1210* in 1889 (K) m.v. 1.

Minor Variant of C. armena typica

1. Plant 2.5–3 dm high; otherwise typical (?). *Sintenis 1210* in 1889 (K) Armenia turcica.

99, *b. Crepis armena longibractea* subsp. nov. Herba perennis 2.5 dm alta; caudex ligneus foliosus, folia omnia caudicalia dense glanduloso-hispidulosa; caulis scapiformis vel 1-furcatus; capitulum medium erectum ad basim dense hirsutum;

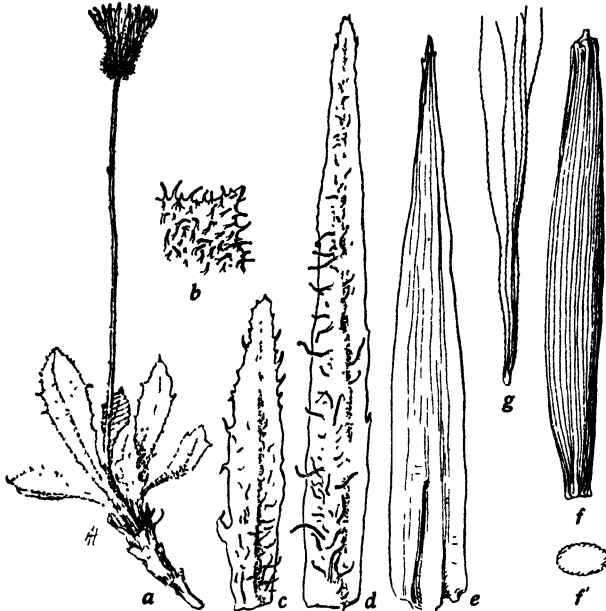


Fig. 145. *Crepis armena longibractea*, from isotype (Bo): a, plant, $\times \frac{1}{2}$; b, lateral tooth and adjacent area of a leaf showing papilliform setae, $\times 8$; c, d, outer and inner involucre bracts, outer face, $\times 4$; e, innermost involucre bract, inner face, $\times 4$; f, achene, with f', cross-section outline, $\times 8$; g, pappus setae, $\times 8$.

involucre campanulatum 12–15 mm longum 6–8 mm latum, squamis exterioribus 10–15 inaequalibus ovatis vel lanceolatis ciliatis et pubescentibus, interioribus 14–18 lanceolatis acuminatis in maturitate carinatis et spongioso-incrassatis; achaenia fusca pallida circa 7 mm longa 1 mm lata fusiformia subteretia circa 20-striata; pappus 5–7 mm longus flavo-albus tenuis mollis 3-seriatus persistens.

Leaves densely hispidulous, with coarse white setae 0.3–0.5 mm long bearing small brown glands; stem scapiform or 1-furcate, fistulose, shortly gland-pubescent near base, glabrescent above, near the head densely hirsute with fine yellow glandular or glandless hairs; involucre 12–15 mm long, 6–8 mm wide at middle, densely hirsute at base, with long curled yellow mostly glandless hairs; outer bracts 10–15, unequal, longest $\frac{1}{2}$ as long as inner ones, outermost ovate, innermost lanceolate, acute, irregularly ciliate on margin, like inner bracts finely pubescent with longer glandless and shorter glandular hairs; inner bracts 14–18, in 2 series, lanceolate, long acuminate, slightly exceeding pappus in mature heads, dorsally keeled, spongy-thickened at maturity; florets lacking in type collection (see m.v. 3); achenes very pale brown, about 7 mm long, 0.8–1 mm wide, fusiform, somewhat

curved, definitely attenuate to the broad summit, narrowed to the calloused hollow base, subterete, about 20-striate, smooth, finely rugulose under lens; pappus 5-6 (7) mm long, yellowish-white. Flowering June-July; flowers yellow in m.v. 3. See fig. 145.

Asia Minor, in E. Anatolia, mountains. The type locality is described as "region alpine de l'aslan Dach (l'un des jucs de l'anti-Taurus) à 12 lieues à l'ESE du mont Argée."

Anatolia: Anti-Taurus reg., Aslan-Dagh, about 70 km east of Mt. Argaeus, alpine, *Balansa* 771, Aug. 6, 1856 (Bo type, UCF, P, PC); Armenia turcica, Sandschak Gümüşchkhane, Mt. Aktasch, *Sintenis* 6184 (UWG) m.v. 2, 3; *ibid.* (B) m.v. (†); Taurus, Farasch, 2000 m, *Siehe* (Hayek); Kurdistan, *Brant and Strangways* in 1840 (K) m.v. 3 (†).

Minor Variants of C. armena longibractea

2. Plant 2.5 dm high, stem 1-furcate; inner involucre bracts scarcely exceeding pappus. *Sintenis* 6184a in 1894 (UWG) Mt. Aktasch, Sandschak Gümüşchkhane, Armenia turcica.

3. Outer involucre bracts shorter and broader than in type, achenes lacking. This is the only specimen of this subspecies in which florets are available, but on account of the absence of achenes and the atypical involucre this material was not used in writing the foregoing description. Corolla 15 mm long; ligule 2.5 mm wide; corolla tube 5 mm long, pubescent with short acicular hairs; anther tube about 4 × 1.5 mm dis.; appendages 0.6 mm long, oblong, obtuse or truncate; filaments 0.5 mm longer; style branches 2 mm long, 0.15 mm wide, yellow. *Sintenis* 6184b in 1894 (UWG) Mt. Aktasch, Szandschak Gümüşchkhane, Armenia turcica. Another collection, probably of this variant, appears to have similar florets; achenes (immature) brown, slightly attenuate upward; pappus 5-6 mm long, dusky, rather coarse, 3-seriate, united at base. *Brant and Strangways* in 1840 (K) Kurdistan.

Relationship

Crepis armena (or the complex represented here) finds its closest relative in *C. heterotricha*, from which it is very distinct in the uniformly colored involucre bracts, the glandular indumentum of the leaves, the more numerous smaller florets, and the broader achenes with longer pappus.

100. *Crepis demavendi* Bornm.

Bull. Herb. Boiss. ser. 2, 7: 435. 1907. (Fig. 146.)

Perennial, 0.7-1.5 dm high; caudex short, woody, 0.3-0.8 cm wide, simple or divided, apparently attenuate into a taproot; caudical leaves numerous, 4-8 cm long, 0.8-1.5 cm wide, oblong-spatulate, acute or obtuse-mucronate, repand-denticulate or entire, very gradually attenuate into a narrowly winged petiole, light green, thin, glabrous, with prominent white midvein; cauline leaves few, all reduced, bractlike, or 1 at first bifurcation 1-3 cm long, lance-linear, acuminate; stems 1-4, very slender, sinuate, scapiform, 1-headed, or 2-3-furcate from near or above the middle, 2-5-headed, glabrous or often gland-pubescent above; peduncles 2-10 cm long, very slender, arcuate, densely gland-pubescent near the head; heads erect, small, about 30-flowered (estimated); involucre nearly cylindric, 8-9 mm long, about 4 mm wide at middle in fruit, pubescent with long glandless and short glandular hairs; outer bracts about 6, very unequal, longest $\frac{1}{2}$ as long as the inner, deltoid to lance-linear, acute; inner bracts 10-12, lanceolate, acute, white-ciliate at apex, glabrous on inner face, becoming weakly carinate dorsally and pale spongy-thickened confluent with the base; receptacle glabrous; corolla about 10 mm long; ligule 1.3 mm wide; teeth 0.5 mm long; corolla tube about 3 mm long, glabrous; anther tube 5 × 1 mm dis.; appendages 0.6 mm long, oblong, obtuse; filaments 0.6 mm longer; achenes stramineous, 4-4.5 mm long, 0.7 mm wide, curved or nearly straight, subterete, the marginal somewhat flattened on inner face and with the median and marginal ribs slightly stronger, 18-20-ribbed, ribs weak, with 4-6 a

little stronger, rounded, finely muriculate under lens; pappus white, 3–5 mm long, 3-seriate, setae unequal, 30–65 μ wide at base, rather stiff but pliable, persistent. Flowering July; flowers pale yellow.

Crepis larensis Bornm., in herb. Barbey-Boissier.

Known only from the type locality, which, in free translation from the Latin, is described by Bornmüller (*loc. cit.*) as follows: "In the narrow place, 'Junesar,' in

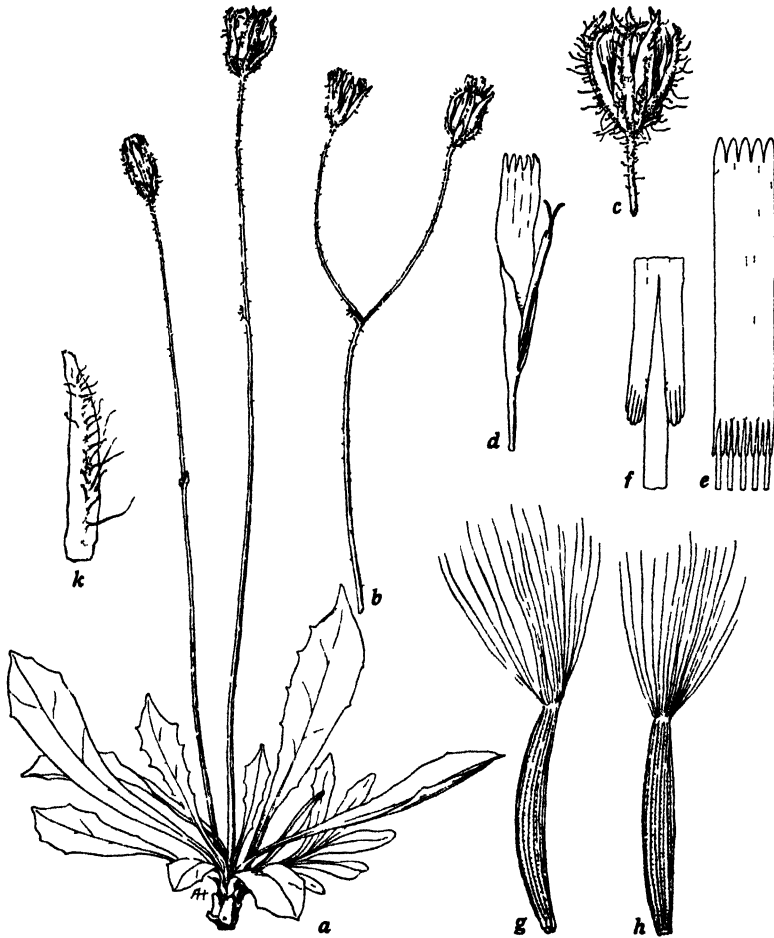


Fig. 146. *Crepis demavendi*, from type collection (Weimar, BB): a, plant, $\times 1$; b, part of a stem with 2 heads, $\times 1$; c, nearly mature head, $\times 2$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, h, 2 achenes with pappus, $\times 8$; k, inner involucre bract, $\times 4$.

Demavend dist. (situated between Yaila Junesar and Karavanserai Bastek), growing in fissures of vertical rock walls, together with rare or new plants: *Draba pulchella*, *Potentilla flaccida* sp. n., *Pyrethrum hololeucum* sp. n., *Erigeron Hyrcanicus* sp. n., *Euphorbia polycaula*, *Triticum rigidum*, *Valeriana sisymbriifolia*, *Oxyria digyna*, *Gypsophila aretioides*, etc.; alt. 2600–2750 m." It is obvious that the record of "Laristan" on the original labels was an error, since the Demavend dist. and the Elburz Mts. are in N. Persia, whereas Laristan is in the S.W. part of the country. Therefore, "Laristan" is omitted in the following citations.

On the type sheet (in herb. Bornm., Weimar) there are 8 plants, of which the

centrally placed one may be designated as the type (cf. photograph in Herb. Univ. Calif.).

Monomorphic.

N. Persia: Elburz Mts., Demavend dist., a narrow vale near Junesar, on rocks, 2700 m, *J. and A. Bornmüller* 7613, July 13, 1902 (Weimar) type; *ibid.* (BB, Ucf), as *C. larensis* Bornm.

Relationship

Crepis demavendi, in the general appearance of the plant, including leaf shape and the very slender scapiform stems, shows most resemblance to *C. armena*. But in size of the heads and achenes, as well as length of the pappus, it is the most reduced species in this section.

101. *Crepis abyssinica* Sch. Bip.

Flora, 22: 20, 1839. (Fig. 147.)

Perennial, 0.3–0.5 dm high; root conical, elongated, woody, strong; caudex 3–8 mm wide, simple or once forked at summit; caudical leaves numerous, up to 3.5 cm

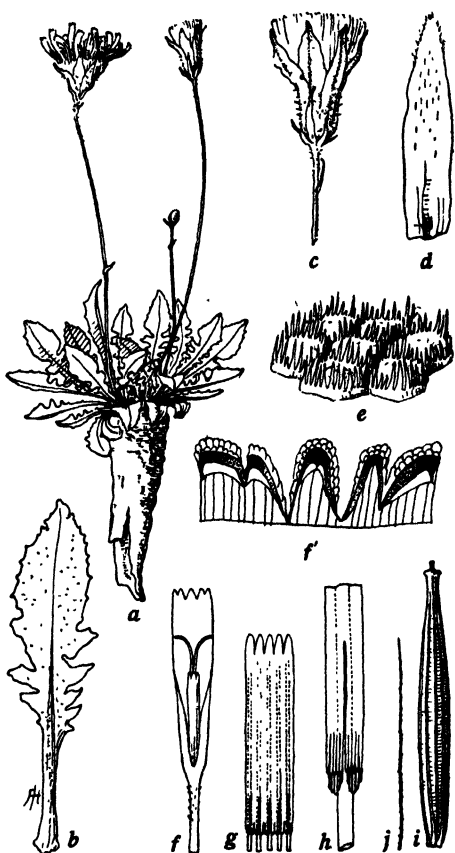


Fig. 147. *Crepis abyssinica*, a, c, f–j, from type (PC); b, d, e, from *Fiori 1896* (Fl): a, plant, $\times 1$; b, leaf, $\times 2$; c, head, $\times 2$; d, inner involucre bract, inner face, $\times 4$; e, detail of receptacle, $\times 25$; f, floret lacking ovary, $\times 4$; g, anther tube, $\times 8$; h, detail of appendages, $\times 32$; i, j, achene and pappus seta, $\times 8$.

long, 0.6 cm wide, oblanceolate, acute or obtuse, apiculate, with a short broadly winged petiole with broader base, denticulate, dentate or runcinate-pinnatifid, becoming conspicuously corneous-mucronate, canescent-tomentose, sometimes pubescent with short white gland hairs on both sides; basal cauline leaves lanceolate or linear, acuminate, the others bractlike; stems several, produced in succession, simple and 1–2-bracteate or 1–3-branched, slender, terete, striate, tomentose and shortly gland-pubescent throughout or near base of head, branches remote, 0.5–6 cm long, pedunculate or 2-headed; peduncles somewhat thickened near head in fruit; heads erect, rather small, about 50-flowered; involucre 7–8 mm high, 2.5–3 mm wide at base in fruit, cylindric-campanulate, canescent-tomentose, gland-pubescent with short fine hairs bearing pale or dark brown glands; outer bracts about 10, unequal, longest $\frac{1}{2}$ as long as inner bracts, 0.5–1 mm wide, lanceolate, acute, dark in mid-region, becoming scarious, lax; inner bracts 7–9, lanceolate, obtuse, with broad yellow membranous margins, ciliate at apex, with dark median dorsal region, with or without a median row of short stout black glandular bristles, ventrally pubescent with white hairs up to 0.2 mm long, becoming strongly carinate and spongy-thickened at full maturity; receptacle alveolate-ciliate, alveolae 0.3 mm wide, cilia strong,

0.1–0.2 mm long; corolla 8.5–10 mm long; ligule 1.2–1.5 mm wide; teeth 0.1–0.3 mm long; corolla tube 2.5–3 mm long, pubescent with papilliform and acicular hairs 0.04–0.12 mm long; anther tube (3.25)3.5 × 0.8(1) mm dis.; appendages 0.6 mm long, oblong, obtuse; style branches yellow, 1.2–1.4 mm long, 0.1 mm wide; achenes dark brown, 5 mm long, 0.5 mm wide, fusiform, subcompressed or subterete, rather strongly attenuate near the narrow (0.2 mm wide) summit, with very slightly expanded disk, constricted at the whitish calloused hollow base, 12–15-ribbed, ribs narrow, rounded, spiculate, especially near summit; pappus white, 3–4 mm long, 2-seriate, setae equal, fine, soft, deciduous. Flowering March–Aug.; flowers yellow, the ligules deep purple on outer face.

Brachydera abyssinica Sch. Bip., ex Schweinfurth, Fl. Aethiop. 1: 283. 1867.

Hieraciodes abyssinicum O. Kuntze, Gen. 1: 345. 1891.

The foregoing description is based on the type and the 11 specimens cited below. The specimen of Rueppell in herb. Cosson is accepted as the type because the accompanying label bears the exact description of locality given in Schultz's original description, whereas the specimen in Herb. Frankfurt gives only "Abyssinia leg. Dr. Rueppell." A photograph of the type is in Herb. Univ. Calif.

Monomorphic.

Central Eritrea, 2000–2600 m. Acc. to Schweinfurth (*op. cit.*), it occurs in "Abyssinia, the land of Schohos and Bogos," and in Massaua, Tigre, Amhara, Gallabat, and Schoa; but no collections known certainly to be from Abyssinia have been seen by me.

Eritrea: (near Adi Caich) between Halai (2590 m) and Temben, *Rueppell* in May–June, 1832 (PC) type; Serae (Arresa) Adi-Ugri, 2000 m, *Fiori 1896*, Mar. 20, 1909 (F1). **Abyssinia (?)** = **Eritrea (?)**: *Rueppell* (Frankfurt) isotype (†); without locality, collected Aug., 1847 (B ex herb. Link) 2 sheets, 6 plants. Although the specimens cited last were determined by Fries as *C. Rueppellii*, they agree very closely with the type of *C. abyssinica*, and they have mature achenes.

Relationship

Crepis abyssinica is closer to *C. xylorrhiza* than any other species in this section; but it is much more reduced in size throughout the whole plant. In habit it resembles *C. Robertioides*, but differs from that species in many characters. Superficially, *C. abyssinica* would pass as a diminutive form of *C. Rueppellii* of sec. 27; but it is very distinct from that species in many characters.

SECTION 12. IXERIDOPSIS

Relationships of the species

The 7 species comprising this section, *C. corniculata*, *C. alaica*, *C. flexuosa*, *C. naniforma*, *C. lactea*, *C. nana*, and *C. elegans*, are glabrous, of low stature, with a slender woody root and caudex, often multiplying from subterranean shoots, with slender branching stems, often forming a tuft or low mound, with small leaves, small few-flowered heads, and terete finely ribbed or striate achenes. All these species except *C. corniculata* and *C. naniforma* have been referred by various authors to *Youngia*, either as a genus or as a subgroup under *Crepis*. The original reference of *C. flexuosa* and *C. nana* to *Youngia* was made by Ledebour (R, 836–838), who copied his description verbatim from de Candolle (192). But de Candolle included in his list of species only *Y. japonica*, the type species of the genus (although not so recognized by him), together with a number of its synonyms and several “species non satis notae,” most of which are species of *Ixeris*. His description includes the following: “achaenia oblonga, nunc compressa nunc saepe in iisdem capitulis subtrigona,” which does not apply to *C. flexuosa*, *C. nana*, and their close relatives, since in these species the achenes are terete or subterete, as in most *Crepis* species. Apparently Ledebour’s inclusion of these species under *Youngia* was based merely on resemblance of the involucre and without consideration of the important differences in the achenes. In their monograph on the genus *Youngia*, Babcock and Stebbins (484: 13–14) have shown that *Youngia* and *Ixeris* are undoubtedly closely related genera, with similar geographical distributions, and that they are well set off from *Crepis* and are still more remote from *Lactuca*.

Sec. **Ixeridopsis** is so named because these 7 species certainly show more resemblance to *Ixeris* than to *Youngia* in the low stature and glabrous herbage, the small often entire leaves, the small few-flowered heads, and especially in the terete achenes which, however, are weakly ribbed or merely striate and neither alate, as in many *Ixeris* species, nor compressed and angular, as in *Youngia*. *Ixeris alpicola* Nakai shows marked similarity to the species of this section in habit, leaves, and involucre; but, like most other species of *Ixeris*, it is characterized by the green anthers and style branches and especially by the strongly ribbed achenes with the inner ones subterete and the marginal somewhat compressed. Cytological evidence supports the segregation of 3 of these 7 species in a section, since their somatic chromosome number, 14, is not found in any other species of *Crepis* and is the same as that of *Ixeris alpicola* (Ishikawa, Bot. Mag. Tokyo 35: 153. 1921). Furthermore, the chromosomes of *I. alpicola* are similar in size and morphology to those of *C. nana*.

Thus, there is morphological and cytological evidence that *C. flexuosa*, *C. nana*, and *C. elegans* are transitional from *Crepis* to *Ixeris*. But, because of their phylogenetic position, they can hardly be considered an ancestral group from which both *Crepis* and *Ixeris* were derived. As has already been pointed out (B., S., and J.: 202), the hypothesis that these 3 species originated through intergeneric hybridization when the 2 genera were in a formative stage is more plausible. The possibility that this entire group of 7 species may have resulted from hybridization between *Ixeris* and *Crepis*, at a time when the present generic divergences were not so strongly developed, is worthy of emphasis.

The evidence from the comparative morphology and geographic distribution of the 7 species gives strong support to this hypothesis. Five of the species are restricted to Central Asia (fig. 148). Three of these, *C. corniculata*, *C. alaica*, and *C. flexuosa*, are the most primitive members of the section and are similar, especially in leaf shape and the definitely tuberculate inner involucre bracts; whereas the

SECTION 12

1. *C. CORNICULATA*
2. *C. ALAICA*
3. *C. FLEXUOSA*
4. *C. NANIFORMA*
5. *C. LACTEA*
6. *C. NANA*
7. *C. ELEGANS*

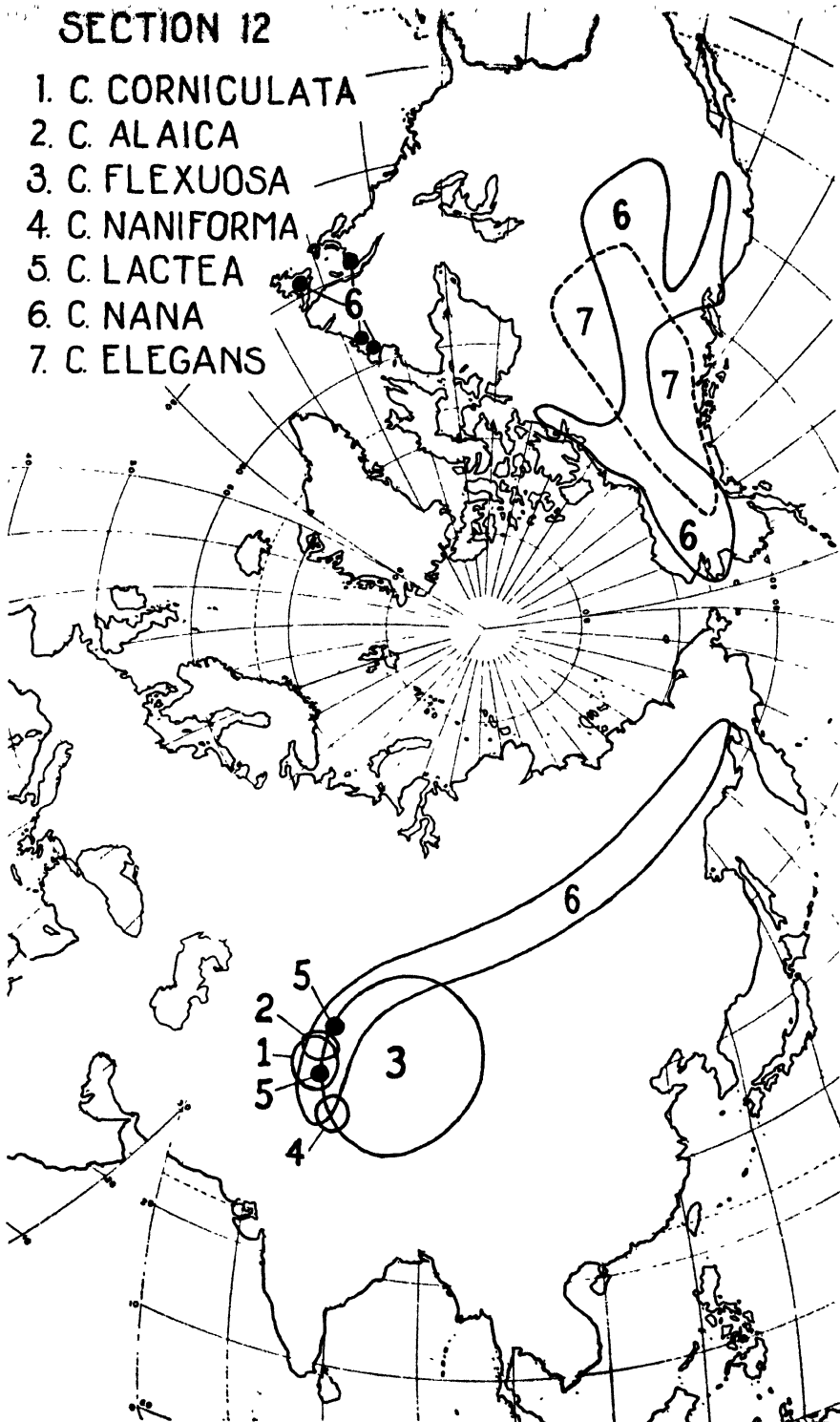


Fig. 148. Geographic distribution of the 7 species in sec. 12. Only two, *C. nana* and *C. elegans*, occur in North America. Single stations are shown by solid circles, but on this map each species occurs at more than one station, although *C. lactea* is known from only two. Based on Goode Base Map No. #01 PC. By permission of the University of Chicago Press.

other 2, *C. naniforma* and *C. lactea*, are intermediate between the first 3 and *C. nana* and *C. elegans*, which are the most advanced of the 7 species. *C. nana* is the most widely distributed species in the whole genus, since it extends discontinuously from the Altai reg. to E. Labrador, Newfoundland, and Gaspé, and, as an alpine species, southward in North America through the Cordillera to Colorado, Nevada, and California, where it occurs occasionally in the Sierra Nevada. *C. elegans* exists only in W. North America from central Alaska southward in the Cordilleran reg. to Montana and Wyoming. *C. elegans*, with its finely beaked achenes, extremely small florets, and adaptation to lower altitudes, is certainly a more advanced species than *C. nana* and was probably derived from *C. nana*. C. W. Sharsmith in his "History of the Development of the Alpine Flora of the Sierra Nevada" (Thesis, filed in archives, Univ. Calif. Library, Berkeley, 1940) classifies *C. nana typica* as a member of the Arctic-Alpine element of the Sierra Nevada of California, and *C. nana ramosa* as an Arctic-Alpine derivative endemic, like *Salix petrophila* var. *caespitosa* and *Arenaria capillaris* var. *compacta*. In fact, *C. nana* is one of about 15 Sierra Nevadan alpine species which appear to be nunatak species. One of these is *Anemone Baldensis*, the occurrence of which, according to Sharsmith, is enough "in itself to establish the former existence of a larger Arctic-Alpine Element which has undergone extensive extinction in the Sierra Nevada." Sharsmith has fixed the chronology of *C. nana typica* (along with many other Sierra Nevadan alpine species) to be between the Pliocene epoch and the Wisconsin stage of glaciation in the Pleistocene. From the present distribution of *C. nana* and of the section as a whole, it is safe to assume a Central Asiatic origin at least as early as the Pliocene and perhaps earlier. Hence, all the evidence concerning this section is entirely consistent with the general hypothesis of a Central Asiatic origin for the genus.

Key to the Species of Section 12

- Plant glabrous, except involucre and peduncles or axils of the leaves, which are canescent-tomentose; inner involucre bracts tuberculate near the apex; cauline leaves as large as the caudal leaves.
- Inner involucre bracts with a prominent corniculate dorsal tubercle near the apex; achenes 4.5 mm long 102. *C. corniculata*, p. 531
- Inner involucre bracts with a small ovoid dorsal tubercle near the apex; achenes 7 mm long 103. *C. alalca*, p. 532
- Plant entirely glabrous; inner involucre bracts not tuberculate, or, if dorsally thickened or obscurely tuberculate near the apex (*C. lactea*), then the cauline leaves bractlike; cauline leaves smaller than the caudal leaves.
- Corolla 10–14 mm long, the ligule about twice as long as the tube; anther tube 3.5–4.5 mm long.
- Stems excessively branched and rebranched, forming an obconical, nearly truncate, many-headed aggregate inflorescence; ligules yellow, with purple teeth 104. *C. flexuosa*, p. 534
- Stems few-branched, forming a conical or corymbiform aggregate inflorescence; ligules reddish-purple or yellow, with red lines on the outer face.
- Ligules yellow, with reddish lines on outer face; achenes 10-ribbed, the ribs rather strong; pappus pale tawny, 6 mm long 105. *C. naniforma*, p. 536
- Ligules reddish-purple; achenes 10-striate; pappus white, 5 mm long 106. *C. lactea*, p. 538
- Corolla 7–9 mm long, the ligule about equal to the tube; anther tube 2.5–2.75 mm long.
- Plant low, tufted or (*C. nana ramosa*) up to 1.8 dm high; root and caudex slender; involucre 10–13 mm long; ligules 1.3–1.5 mm wide; achenes columnar, slightly or strongly attenuate at the apex, 10–13-ribbed, the ribs rounded, smooth 107. *C. nana*, p. 539

Plant taller, 1.5–2.5 dm high; root and caudex wider; involucre 8–10 mm long; ligules 1 mm wide; achenes with a delicate beak $\frac{1}{4}$ as long as the body, 10-ribbed, the ribs narrow, spiculate 108. *C. elegans*, p. 545

102. *Crepis corniculata* Rgl. et Schmalh.

Ex Regel, Pl. Nov. Fedtsch., in Fedtsch., Reise Turkest. 18: 54. 1881;

Izvest. Imp. Obsch. Ljub. Est. 34(2): 54. 1882. (Fig. 149.)

Perennial (?), up to 3.5 dm high, glaucous and glabrous, except the involucre, peduncles, and (?) bifurcations of the stem, which are canescent-tomentulose; stem

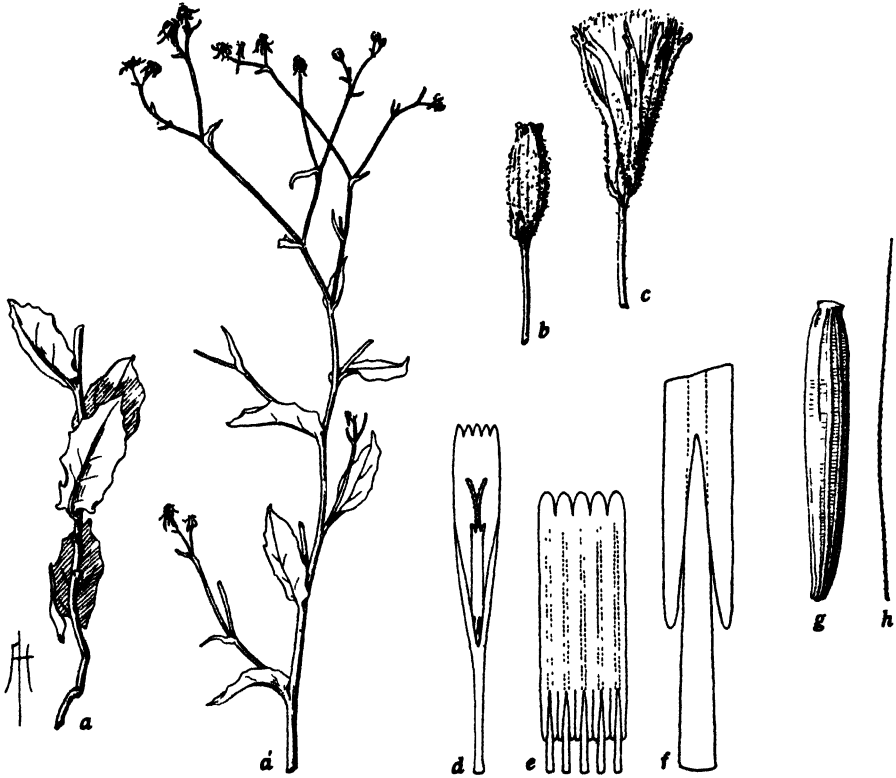


Fig. 149. *Crepis corniculata*, a, a', g, h, from Regel in 1882 (BB); b–f, from Lipsky in 1896 (Lenin): a, a', plant, $\times \frac{1}{2}$; b, young head, $\times 2$; c, nearly mature head, $\times 2$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, h, achene and pappus seta, $\times 8$.

erect, flexuous, terete, striate, remotely leafy, and paniculately branched from near base, or (ex descr.) simple, with bractlike leaves; caudical leaves ephemeral, not seen; cauline leaves sessile, ovate-oblong, obtuse-mucronate, or oblong-acute, repand-denticulate, \pm amplexicaul or subauriculate, pergameneous, glaucous, uppermost linear, bractlike; branches short, simple, 1-headed, or furcate, 2–4-headed; peduncles 0.1–2 cm long, somewhat thickened near head; heads erect, medium, few-flowered (about 12 ?); involucre cylindric-campanulate, 9–10 mm high, about 3 mm wide near base at maturity, canescent-tomentose, bracts densely white-ciliate at apex; outer bracts about 7, unequal, longest 2 mm, lance-linear, obtuse; inner bracts 9 or 10, lanceolate, obtuse, with a prominent dorsal corniculate tubercle near apex, becoming carinately thickened dorsally, ventrally glabrous, ultimately reflexed; receptacle alveolate, glabrous; corolla about 11 mm long; ligule about 2 mm wide;

teeth 0.5 mm long, acute; corolla tube 4 mm long, glabrous (?); anther tube 4×1.5 dis.; appendages 0.7 mm long, lanceolate, acute; filaments short; achenes yellowish, 4.5 mm long, 0.6 mm wide above middle, subterete, constricted at summit below the expanded pappus disk, gradually attenuate from middle to the very narrow base, 10-ribbed, ribs narrow, rounded, finely spiculate under lens; pappus white, 6 mm long, copious, multiseriate, rather stiff, fine, coming away in clumps, persistent. Flowering Aug.-Sept.; flowers yellow.

Hieraciodes corniculatum O. Kuntze, Gen. 1: 345. 1891.

W. Asia, in the Pamir-Alai Mts., 2200–3000 m alt. Type locality: Kokania, Alai Mts., 2424 m (O. Fedtschenko in 1871). Other localities given by Fedtschenko (Beih. Bot. Centralbl. 40: 204. 1923): Trans-Alai-Kette, Altyn-Masar (Newessky); oberhalb Altyn-Masar (B. Fedtschenko); Abhang des Passes Ters-agar (Newessky); bei Imtz, im Roschan (A. Regel).

Although the type has not been seen by me, the species is apparently monomorphic.

Turkestan: Murgab R. valley, *A. Regel* in 1882 (BB, K, UCf, B); E. (?) Turkestan, "Yurkand Expedition, 1870," *Henderson 444* (K); Buchara Prov., *Lipsky* in 1896 (Lenin, UCf). **Afghanistan:** Wakhan Prov. (extreme south of Pamir), Pamir Mts., Langarkisht, Pandsch R., among alders, *Taulsen 1326* (B).

Relationship

Crepis corniculata exhibits sufficient resemblance to *C. alaica* in habit, leaves, involucre, flowers, and fruits to indicate a definite relationship. Through *C. alaica*, then, this species is related to *C. flexuosa* and, less closely, to the other members of this section. The fact that Taulsen's specimen, cited above, was collected among alders is sufficient to indicate a water relationship for this species similar to that of other members of the section.

103. *Crepis alaica* H. Krasch.

Acta. Inst. Bot. Acad. Sci. U. S. S. R. ser. I. 1: 182. 1933. (Fig. 150.)

Perennial, 0.5–1 dm high, entirely glabrous, except for inconspicuous white wool in the axils of the leaves; root or subterranean stem very slender, elongated, sometimes with remnants of old leaves and vegetative buds several cm below the leafy caudex; caudical leaves 1–2.5 cm long, spatulate, blade roundish to elliptic, abruptly attenuate into a broadly winged petiole equal to blade with broad clasping base, thick, chartaceous, glaucous, purplish, irregularly sinuate-dentate, teeth acute, cartilaginous-mucronate, margin involute; cauline leaves similar, narrow-elliptic or lanceolate, sessile, semiamplexicaul, gradually reduced upward, extreme uppermost foliaceous, not bractlike; stem slender, terete, sinuate, internodes short, branches divaricate, short, few-headed, congested, cymose-corymbiform; peduncles very short, sulcate; heads erect, small, 9–10-flowered; involucre cylindric-campanulate, 10 mm long, 2 mm wide near base in fruit; outer bracts 5–7, with 1–2 subtending, rather loose, spreading, unequal, longest $\frac{1}{4}$ – $\frac{1}{3}$ as long as inner bracts, ovate-lanceolate, acute, reflexed, dark green, \pm ciliate, yellowish below, with a strong narrow keel, thicker at base; inner bracts 9–10, lanceolate, acute, in 2 ranks, inner ones broadly membranous-margined, ventrally glabrous, dorsally dark green toward summit, yellowish toward base, with a narrow median yellow keel extending almost to summit and terminating in a thickened dark-tipped tubercle just below the thin white-ciliate often purplish apex; receptacle areolate-fimbriate, fimbriae low, fleshy, glabrous; corolla 12 mm long; ligule 2.5 mm wide, pale yellow tinged purple; teeth 0.3–0.5 mm long, deep purplish-red; corolla tube 4–4.5

mm long, beset with stalked conical acute trichomes 0.05 mm long; anther tube 5×1.3 mm dis.; appendages 1 mm long, oblong, truncate; filaments extremely short, scarcely exceeding appendages; style branches 2 mm long, 0.2 mm wide, yellow; achenes golden brown, 7 mm long, 0.5 mm wide, fusiform, slightly narrowed above the truncate calloused base, strongly attenuate to the narrow summit, with expanded pappus disk, 10-ribbed, ribs smooth, narrow, with wider spaces between;

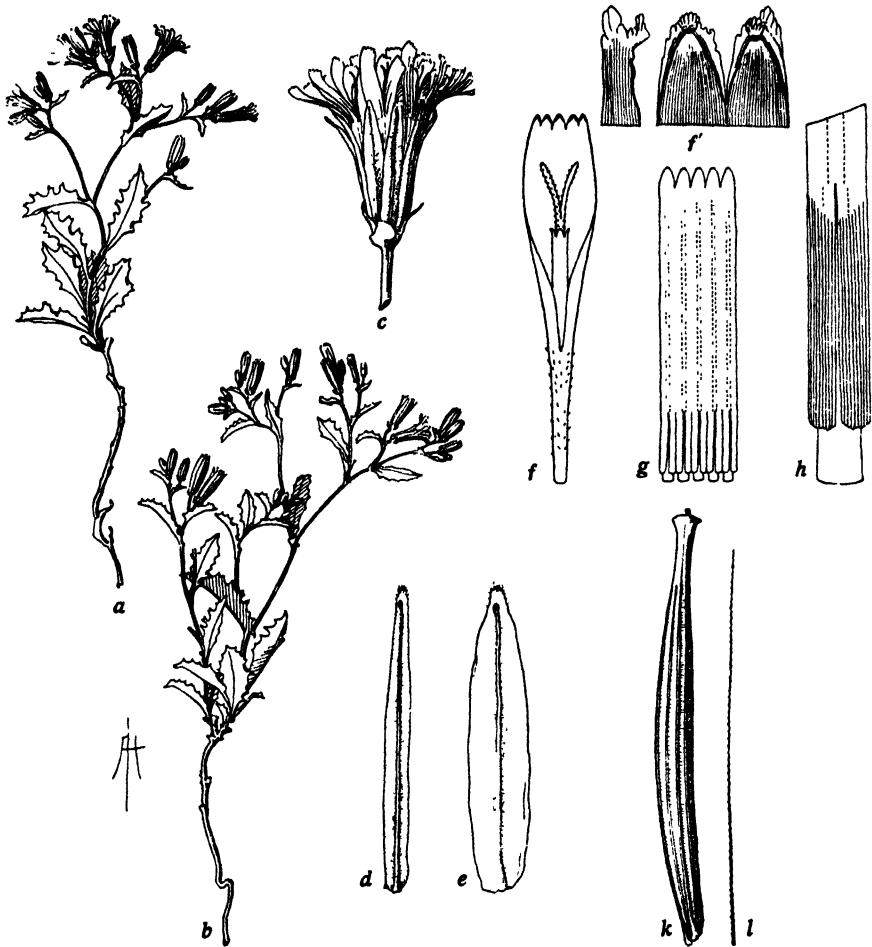


Fig. 150. *Crepis alaiica*, from Dessjator 1466 (Lenin): *a*, *b*, plants, $\times \frac{1}{2}$; *c*, head, $\times 2$; *d*, *e*, inner bracts, outer face, $\times 4$; *f*, floret lacking ovary, $\times 4$; *f'*, details of ligule teeth, $\times 25$; *g*, anther tube, $\times 8$; *h*, detail of appendages, $\times 32$; *k*, *l*, achene and pappus seta, $\times 8$.

pappus white, up to 6.5 mm long, copious, multiseriate, at maturity unequal in length and thickness of the setae, rather brittle, persistent. Flowering June–July; flowers yellowish-purple, becoming deeper purple with age.

Turkestan, Ferghana reg., Ali R. valley, and in the Alai and Transalai Mts.

Monomorphic.

Known to the present writer from only 1 collection, which is accepted as typical.

Turkestan: Valley of the Alai R., gravelly banks of the Min-jar, the left fork of the Kysyl-su R., Dessjator 1466 (Lenin). Kraschenninikov (*loc. cit.*) lists the following additional collections: **Tadzhikistania:** in the highest Alai Mts., Togus-kungei R., rocky banks, Korshinsky in 1895; Arcza-bulak, Kuschakewicz in 1878; Transalai Mts., between Bordoba and Saratasch, O. and B. Fedtschenko in 1901.

The statement of Kraschenninikov (*loc. cit.*) that the area of this species lies outside the distribution of *C. flexuosa* is not correct, and it is to be noted that *C. nana* also occurs in the mountains of Central Asia, as does *C. lactea* (see fig. 148).

Relationship

Crepis alaica is a very distinct species, but it is closely related to *C. lactea* on the basis of floral characters. Thus, it is connected with *C. nana* and *C. elegans*. However, it shows more resemblance to *C. flexuosa* in habit, leaves, and achenes than to any of the above three, although it is also very distinct from the latter. The tuberculate inner involucre bracts, leaf shape, and white wool in the leaf axils suggest a connection with *C. corniculata*. In fact, *C. alaica* may be considered a connecting species between *C. corniculata* and the other species of this section.

104. *Crepis flexuosa* (DC.) Benth. et Hook. f.

Gen. Pl. 2: 515. 1873; C. B. Clarke, Comp. Ind. 254. 1876. (Pl. 11. Fig. 151.)

Glabrous perennial, 0.6–3 dm high, reproducing vegetatively from root sprouts as well as from seeds; root very slender, elongated, producing fine fibrous roots 5–10 cm below surface which generate adventitious buds; caudex simple at summit in young plants, becoming woody, \pm divided, and suffrutescent in old specimens; caudical leaves up to 6 cm long, 2 cm wide, long-petioled, spatulate, obovate or oblanceolate, sinuate-dentate, runcinate-pinnatifid or pinnately parted, with denticulate acute segments, glaucous; cauline leaves similar or linear, sessile, uppermost bractlike; stems very numerous in well-developed specimens, dichotomously and divaricately excessively branched, forming an obconical mass 1–3 dm wide at the nearly truncate top, the branches slender, rigid; peduncles 0.5–1 cm long, very slender; heads erect, small, narrow, 9–13-flowered; involucre cylindric, 7–10 mm long, 2–3 mm wide near base, pale or very dark green; outer bracts 8, very small, unequal, in 2 series, with 1 or 2 subtending ones, ovate or lanceolate; inner bracts 9 or 10, equal, lanceolate, acute, in 2 series, inner ones broadly scarious-margined, ciliate at apex, glabrous within, becoming carinately spongy-thickened, ultimately reflexed; receptacle areolate, glabrous; corolla 10 mm long; ligule 2 mm wide; teeth 0.4–0.8 mm long, oblong, acute; corolla tube 4 mm long, glabrous or sparsely beset with minute conical trichomes; anther tube 4×1.5 mm dis.; appendages 0.75 mm long, lanceolate, acute; style branches 1 mm long, yellow; achenes yellowish, 4.3–5.5 mm long, 0.4–0.5 mm wide, subterete, fusiform, \pm attenuate to both ends, sometimes strongly constricted below the expanded pappus disk, 10-ribbed, ribs narrow, rounded, well separated in fertile fruits, faintly rugulose, broadened, and calloused at the narrow base; pappus white or sometimes yellowish, 4–5 mm long, 1-seriate, very fine, soft, deciduous. Flowering June–Oct.; flowers yellow, with purple ligule teeth. Chromosomes, $2n = 14$.

Prenanthes polymorpha var. *flexuosa* Ledeb., Fl. Alt. 4: 145. 1833.

Barkhausia flexuosa DC., Prod. 7: 156. 1838.

Youngia flexuosa Ledeb., Fl. Ros. 2: 838. 1844–1846.

Youngia glauca Edgew., Trans. Linn. Soc. 20: 79. 1846.

Crepis glauca Benth., Gen. Pl. 2: 515. 1873.

Hieraciodes flexuosum O. Kuntze, Gen. 1: 346. 1891.

Central Asia, in the mountains of Pamir and in the Tien Shan Mts., Semipalatinsk and Outer Mongolia from Lake Balkash to the Altai Mts., N.W. China in Kansu Prov., W. Tibet and the W. Himalaya Mts.; gravelly plains, sandy river bottoms, mountain terraces and valleys, crevices of rocks, and shale slopes, 1750–5200 m alt.

This species is fairly constant throughout its range, except for minor variations in degree of attenuateness of the achenes and especially in the depauperate specimens from very high altitudes or adverse environments (see m.v. 1 and 2). The disappearance of the caudical leaves and the intricate branching in old plants give them a very different appearance from juvenile specimens. It was this difference in the early and later leaves, presumably, that caused the recognition of var. *lyrata* Schrenk (Fisch. et Mey., Enum. Pl. Nov. 39. 1841). Acc. to Fedtschenko (209),

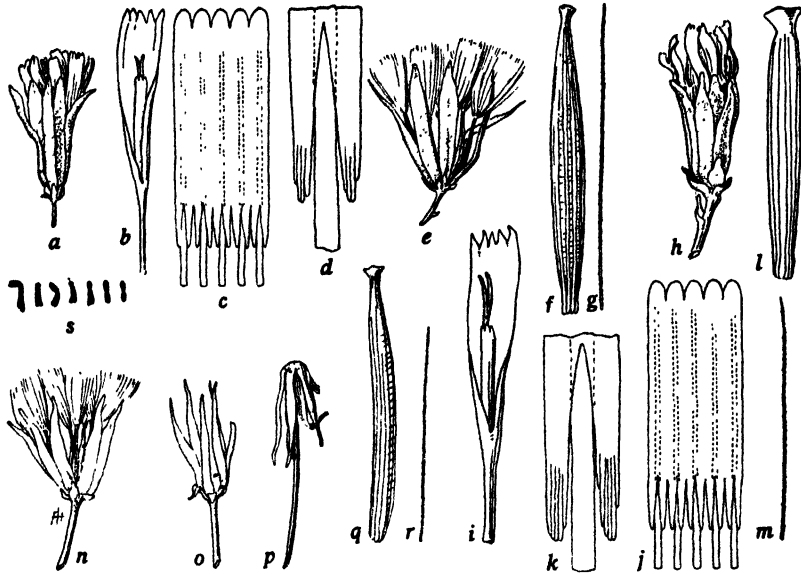


Fig. 151. *Crepis flexuosa*, a-d, from Thomson in 1847 (K, cf. Fl. Brit. Ind. 3: 394); e-g, from Duthie 13707 (UWG); h-m, from Deasy 862 (K); n-r, from Schrenk ex herb. Keck (UWK); s, from hort. genet. Calif. 2983 (grown from seeds received from Lepsinsk dist., Dzungaria, through Dr. M. Navashin): a, young head, $\times 2$; b, floret lacking ovary, $\times 4$; c, anther tube, $\times 8$; d, detail of appendages, $\times 32$; e, immature head, $\times 2$; f, g, achene and pappus seta, $\times 8$; h, head, $\times 2$; i, floret lacking ovary, $\times 4$; j, anther tube, $\times 8$; k, detail of appendages, $\times 32$; l, achene and pappus seta, $\times 8$; m, nearly mature head, $\times 8$; n, part of a mature head, $\times 2$; o, old head showing reflexed bracts and naked receptacle, $\times 2$; p, q, r, achene and pappus seta, $\times 8$; s, somatic chromosomes, $n = 7$, $\times 1250$.

C. Winkler recognized var. *corniculata* and var. *gigantea*, specimens of which have not been seen by me. Cornicles on the inner involucre bracts would be atypical for this species, but if such a form exists it merely emphasizes the intermediate position of *C. flexuosa* between *C. altaica* and *C. corniculata*, on one hand, and the other species in this section, on the other. The identity of the var. *gigantea* is in doubt. It was reported by O. Fedtschenko (Fl. Pamir 137. 1903) as occurring, together with the typical form, in Pamir between the Pamir (Pamirski ?) and Kara-su posts. It may be merely a well-developed old plant like Stewart's no. 20586 (cited below) from Punjab. There is no specimen of *Barkhausia flexuosa* in herb. DC., but an authentic specimen in Herb. Leningrad has been seen by me. Photographs of the type materials of both *Youngia glauca* Edgew. and *C. glauca* Benth. are in Herb. Univ. Calif., and U.S. Nat. Herb.

Semipalatinsk: Arkaul and Tschingistan Mts., Meyer (Lenin) type; Altai, Ledebour ? (Mo); Songoria, near Lake Balkash, Schrenk (UWK) m.v. 2. **Outer Mongolia:** Altai Mts., Baga Bogdo, cottonwood terrace, Chaney 278 (UC). **China:** Kansu Prov., vicinity of Lichen, Ching 310 (US) m.v. 1. **Turkestan:** Tien Shan Mts., near Lake Issyk Kul, Tekes R. valley, Regel 1026 (B, K); Tamis, Aksu, Kuschakewies in 1878 (K, US); Tairam, Regel in 1878 (K). **Tibet:** temperate and alpine regions, gravelly plain, Thomson in 1847 (K, Ucf), as *C. glauca* Benth.; Parang Valley,

Shayuk Valley, prairie below Sialo, *Thomson* in 1847 (K, B, UC); damp places, 34° 21' N., 82° 6' E., 4910 m, *Deasy* 857, 862, 878 (K, UCf) m.v. 1; Himis Shupka, Ladak, *Stewart* in 1912 (UC). **Kumaun:** Himalaya Mts., Niti, *Edgeworth* in 1844 (K), as *Youngia glauca* Edgew.; Kumaon, Milam Glacier, *Strachy and Winterbottom* in 1840 † (K). **Kashmir:** Dras Valley, *Duthie* 13707 (UWG, UCf, Calcutta); Zoji Pass to Matayan, *Stewart* 7489 (UC); Ladak, Tsakzhun Tso, in sand, *Koelz* 2408 (US). **Punjab:** Kangra, Lahul, Bhaga Valley, Ghantal, *Chand* 122A (US); Kichu, Spiti, *Gill* 1935 (DD); Baltistan, Thalle La, *Stewart* 20586 (UC); Satpura Nullah, above Skardu, *Stewart* 20398 (UC); Shyok Valley, Blaghar to Kuru, *Stewart* 20848 (UC).

Minor Variants of *C. flexuosa*

1. Low tufted plants; stems short, the heads congested somewhat as in *C. nana*; achenes 4.5 mm long, moderately attenuate, with unusually broad pappus disk. *Deasy* 857, 862, 878 (K) damp places, 4910 m, 34° 21' N., 82° 6' E.; *Thorold* 70 (K) wide stony valleys, 5211 m, N.W. Tibet; *Ching* 310 (US) vicinity of Lichen, 1750–2050 m, Kansu Prov., China. (Fig. 151, h–m.)

2. Involucre only 6 mm high and 1 mm wide at base; achenes 4.3 mm long, very slender; pappus 4 mm long. *Schrenk* (UWK), near Lake Balkash, Songoria, Semipalatinsk, Siberia. (Fig. 151, n–r.)

Relationship

Crepis flexuosa has as its nearest relatives 2 closely related groups of species, viz., *C. altaica* and *C. corniculata*, on the one hand, and *C. naniforma*, *C. lactea*, *C. nana* and *C. elegans*, on the other hand. Its chromosomes are similar to those of the latter two species, but it differs strikingly from both groups in floral and vegetative characters. Certain specimens of *C. flexuosa* have furnished evidence indicating the primitive relationships of this section. In plants collected in Kashmir at about 2800 m (*Stewart* 20586), the much-branched caudex was woody and was covered with a grayish-brown cortex bearing the marks of old leaf scars. One of these plants appeared to be at least 7 years old, and it was probably older. Thus, under favorable conditions, this species is a strong, woody-based perennial—a definite mark of primitiveness.

105. *Crepis naniforma* sp. nov.

(Fig. 152.)

Herba perennis 0.8–1 dm alta omnia glabra; folia caulina petiolata spathulata sinuato-denticulata; caulis sinuatus simplex vel furcatus cum 2–8 capitulis; capitula parva 9–13-flora; involucre cylindrica 10–11.5 mm longa nigro-virida, squamis exterioribus 3–5 brevis linearibus vel ovatis, interioribus 7–8, oblongis in maturitate carinatis et spongioso-incrassatis; receptaculum areolatum glabrum; corolla 11–12 mm longa, tubo 4–5 mm longo glabro; antherae 3.75 mm longae; rami styli 1.25–1.75 mm longi flavi; achaenia fusca pallida 5.5–6.5 mm longa 0.5–0.6 mm lata subteretia fusiformia 10-costata; pappus fuscus 6 mm longus 2–4 seriatus persistens.

Perennial, 0.8–1 dm high, entirely glabrous; caudex very slender, elongated, with remnants of old leaves and axillary buds several cm below crown, leafy at crown; cauline leaves all long-petiolate except those at bifurcations of the inflorescence, which are sessile, linear, or bractlike; lower cauline leaves 4–9 cm long, 0.6–1.6 cm wide, spatulate, the blade short, elliptic to ovate or obovate, obtuse, sinuate-denticulate, the small teeth acute, corneous-mucronate, the margin narrowly involute, petiole 2–4 times longer, alate; stem sinuate, simple, 2-headed, or dichotomously 2-branched, the branches elongated, 2–4-headed; peduncles 0.5–3 cm long, slender; heads erect, small, 9–13-flowered; involucre cylindric, 10–11.5 mm long, 2–4 mm wide at middle in fruit, dark green; outer bracts 3–5 with 2 or 3 subtending, linear to ovate, acute, very short or rarely the longest $\frac{1}{4}$ as long as the inner; inner bracts 7–8, oblong, acute or obtuse, glabrous on both sides, dorsally dark green except the broad membranous margin, with a median nerve not notably thickened at the apex, becoming carinate, brownish, and spongy-thickened at base

in fruit; receptacle areolate, glabrous; corolla 11–12 mm long; ligule 2 mm wide; teeth 0.25–0.5 mm long, prominently glandular; corolla tube 4–5 mm long, glabrous; anther tube 3.75 × 1 mm dis.; appendages 0.8 mm long, oblong, acute; filaments only 0.4–0.5 mm longer; style branches 1.25–1.75 mm long, 0.15 mm wide, yellow; achenes (fully mature) light brown, 5.5–6.5 mm long, 0.5–0.6 mm wide, subterete, fusiform, moderately attenuate to the paler obconical apex and pappus disk,

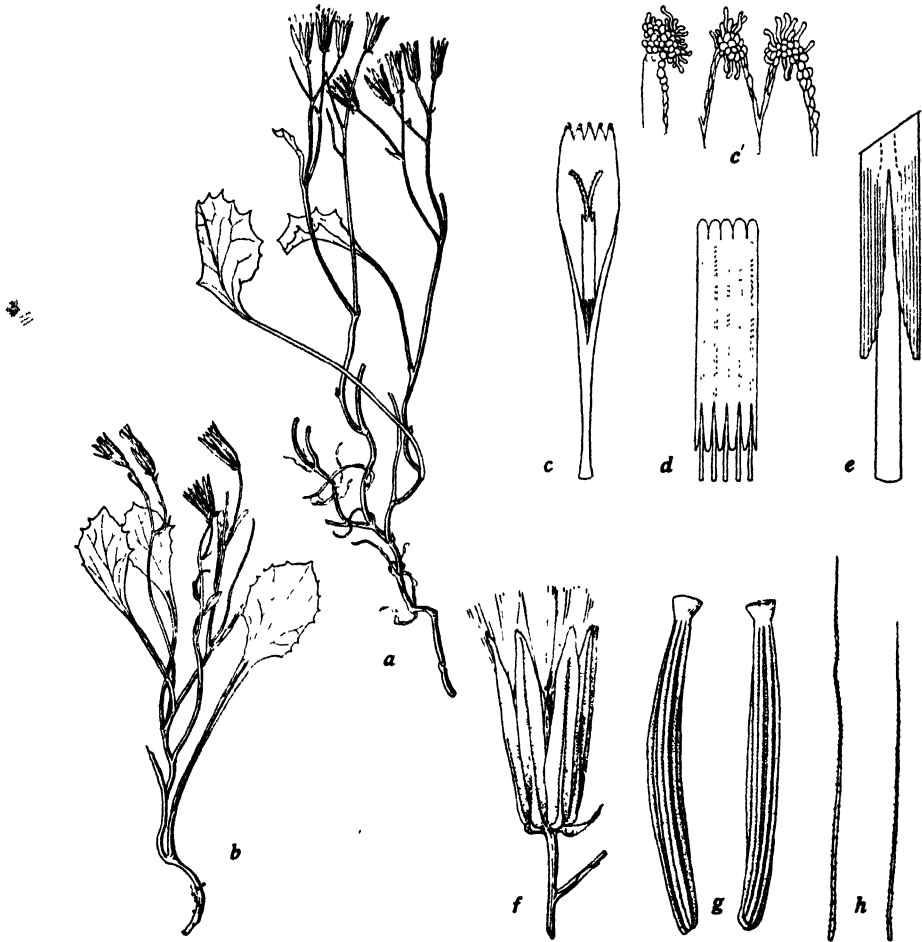


Fig. 152. *Crepis naniforma*, from type collection (B, US): a, b, parts of a plant, × 1; c, floret lacking ovary, × 4; c', detail of ligule teeth, × 25; d, anther tube, × 8; e, detail of appendages, × 32; f, fruiting head, × 2; g, h, achene, 2 views, and smallest and largest pappus setae, × 8.

slightly constricted at the closed calloused base, 10-ribbed, ribs rather prominent, close, with narrow spaces between, rounded, muriculate; pappus pale tawny, 6 mm long, copious, 2–4-seriate, unequal in length and thickness of the setae, rather stiff but pliable, persistent. Flowering Aug.–Sept.; flowers yellow, with lines of reddish-purple on outer face of ligules.

S. Kashmir and N.E. Punjab, at elevations from 3000 to 5000 m, on shale slopes and river sands. Known to me only from the 3 stations cited below.

Monomorphic.

Kashmir: Ladak, Kangi La, on shale slope with no other plants, 4848 m, *Koels* 2846 (B, UCf, US, NY, DD) type and isotypes; Zanskar, Rangdum, in sand on river bottom, 3030 m, *Koels* 2879a (B, NY). **Punjab:** Kangra, Lahul, Serchu, Rachogbar, 3939 m, *Koels* 6666 (US, UCf).

Relationship

Crepis naniforma is intermediate between *C. alaiica* and *C. lactea*. From *C. alaiica* it is sharply distinguished by having all the cauline leaves petiolate except those bractlike ones subtending the peduncles; by the 2-branched, few-headed inflorescence; by the dark green involucre and absence of a tubercle on the inner bracts; by the glabrous corolla tube and differences in the anther tube, the shorter achenes with stronger ribs, and the definitely tawny or pale brownish pappus. From *C. lactea* it is sharply set off by the dentate leaves, the larger involucre, the complete absence of a tubercle near the apex of the inner bracts, the strongly ribbed achenes, and the tawny pappus, as well as the flower color and various floral details. It is even more distinct from *C. corniculata* and *C. flexuosa*, as well as from *C. nana*, which it superficially resembles.

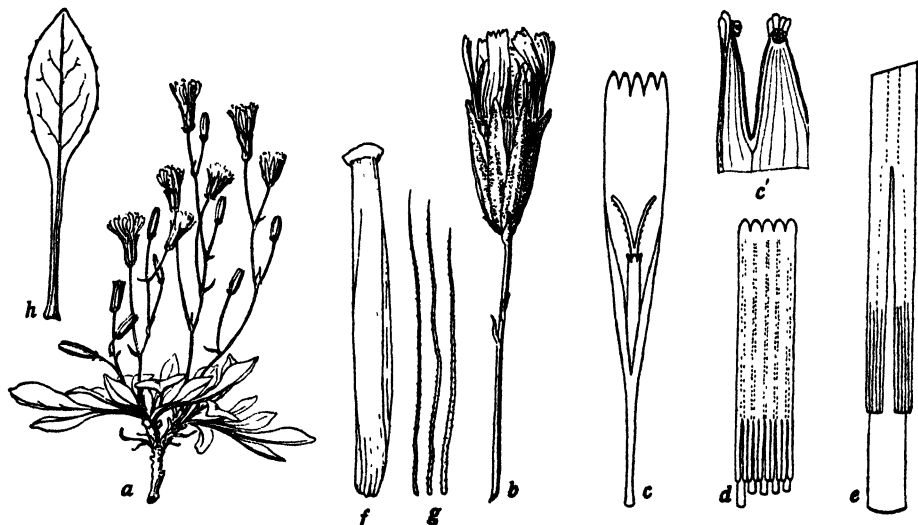


Fig. 153. *Crepis lactea*, a–e, from *Kuschakewicz* in 1878 (K); f–h, from isotype (UC 602799): a, plant, $\times \frac{1}{2}$; b, head and peduncle, $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule teeth, $\times 25$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, nearly mature achene, $\times 8$; g, pappus setae showing variation in width, $\times 8$; h, caudical leaf, $\times 1$.

106. *Crepis lactea* Lipsch.

In Fedde, Rep. Spec. Nov. Veg. 42: 159. 1937. (Fig. 153.)

Tufted glabrous perennial, 0.5–0.9 dm high, with slender vertical or creeping subterranean stems arising from the thicker deeper root; caudex short, densely leafy, \pm ramose; caudical leaves up to 6 cm long, 1 cm wide, spatulate, the blade elliptical or ovate, acute or obtuse, entire or sinuate-denticulate, abruptly attenuate into a long or short narrow petiole, glaucous; stems several, cymosely branched beginning near base, leafy, the lower leaves like caudical ones, upper leaves reduced, bractlike; branches very slender, mostly pedunculate; peduncles 0.5–3 cm long, filiform; heads on old plants numerous, borne well above the leaves, erect, 10–12-flowered; involucre 9–10 mm high, cylindrical; outer bracts about 5, with 2–4 subtending ones, very short, lanceolate or ovate, acuminate, brown-ciliate at apex; inner bracts 8, lanceolate, acute, white-ciliate at tip, membranous-margined, glabrous within, with a brown median dorsal stripe or nerve, which is elevated or obscurely tubercular toward apex of bract, becoming keeled and spongy-thickened at base in fruiting heads; receptacle areolate, glabrous; corolla 11–14 mm long; ligule 2–2.4 mm

wide; ligule teeth 0.25–0.7 mm long; corolla tube 3–4 mm long, glabrous; anther tube (3.5)4.25 × 1 mm dis.; appendages 0.6–1 mm long, narrow, truncate; filaments 0.1–0.7 mm longer; style branches 1.5–2.5 mm long, 0.1–0.15 mm wide, obtuse, yellow; achenes (nearly mature) 5–6 mm long, 0.6 mm wide, stramineous, columnar, more attenuate toward summit, with well-expanded pappus disk, abruptly constricted at the calloused base, 10-striate, striae rounded, smooth; pappus white, 5 mm long, 3-seriate, the setae coming away in clumps, persistent. Flowering July–Aug.; flowers light reddish-purple.

Youngia pygmaea Ledeb. var. *purpurea* C. Winkl., in Fedtsch., Fl. Pamir leg. 1901, B. A. et O. A. Fedtsch., Mosqua, 47. 1904; O. Fedtsch., Fl. Pamir, 137. 1903.
Youngia (Crepis) purpurea Lipsch., loc. cit., non M.B.

The type is at the University of Moscow.

E. Russian Turkestan, in Pamir and the W. Tien Shan Mts., 3100–4575 m. In addition to the stations cited below, O. Fedtschenko (Fl. Pamir 137. 1903), under *Youngia pygmaea* var. *purpurea*, gives 3 other stations in Pamir, viz., Kok-Sai, Kar-Art, and Akbaital. At the last place, it occurred at 4575 m alt. in association with *C. nana typica*.

Monomorphic.

Turkestan: Pamir, Lake Kara-kul, rocks, *Lipschitz* 818, Aug. 12, 1931 (UC) isotype, flowers and fruits; Chargosch Pamir (= Pamir-Khargoshi), *Kuschakewicz* in 1878 (K); E. Turkestan, Tien Shan Mts., Ak-sai R., waterworn rocks, 1381 m, *Regei* in 1882 (K).

Relationship

Crepis lactea simulates *C. nana typica* in habit and general appearance, but it is very distinct in its much longer, light red corolla and its long anther tube with longer truncate appendages. If its mature achenes are merely striate, as seems likely, this is another distinctive character. This species is intermediate between *C. naniforma* and *C. nana*. Its habit, floral characters, and tendency to have a tubercular dorsal thickening near the apex of the inner involucre bracts suggest a connection also with *C. altaica*.

107. *Crepis nana* Richards.

Bot. App. of Franklin, 1st Jour. ed. 1, 746 (18 in repr.). 1823;
 ed. 2, 757 (29 in repr.). 1823. (Figs. 154, 155.)

Glabrous perennial with a slender vertical or creeping subterranean stem or stems arising from a taproot; caudex short, densely leafy, or elongated, ± ramose; caudical leaves spatulate, the blade orbicular, elliptical-obtuse or ovate-acute, entire to lyrate-pinnatifid with few lateral lobes, abruptly attenuate into a long or short narrow petiole, glaucous, often purplish; heads numerous, erect, narrow, 9–12- (mostly 11)-flowered, borne among the leaves in a tuft on short pedunculate branches or well above the caudical leaves on elongated 2–4-headed leafy branches; involucre cylindrical; outer bracts 5–8, unequal, very short or the innermost nearly $\frac{1}{3}$ as long as inner bracts, ovate or lanceolate, acute; inner bracts 10, equal, oblong, narrowed near the obtuse purplish ciliate apex, scarious-margined, becoming carinately spongy-thickened near base; receptacle areolate-fimbriate, glabrous; florets small; ligule very short, yellow tinged purple on outer face, at least the teeth; anther tube short, with long narrow acuminate appendages; style branches short, yellow; achenes golden brown, subterete, columnar, slightly constricted or definitely attenuate at summit or with a very short slender beak, narrowed above the small hollow calloused base, 10–13-ribbed, ribs rounded, smooth or rugulose;

pappus white, 4-6 mm long, 3-seriate, the setae fine, soft, falling away singly. Flowering May-Sept.; flowers purplish-yellow or bright yellow.

Arctic and alpine, this is the most widely distributed species in the genus. It occurs in the mountains of Central Asia from Kashmir and Pamir to Altai and eastward to Kamchatka; in North American arctic regions at scattered locations from Alaska to Gaspé Pen.; and on high elevations in the Rocky Mountains and the higher ranges of Utah, Nevada, and the Pacific Coast states. Although only 1 spec. has been seen by me from the Pamir-Kashmir reg., others have been reported by O. Fedtschenko (Fl. Pamir 137. 1903) and Fedtschenko (209). Acc. to Sharsmith (1940), this species occurs in California on scree slopes in granitics, metamorphics, and unaltered volcanics on both glaciated and unglaciated surfaces.

Usually sporadic on gravel or loose rocks, often near melting snow or glaciers, sometimes on sand bars along high mountain streams, this remarkable little plant is adapted to most rigorous conditions, without having developed any obvious morphological adaptive features other than the deep-rooted, stoloniferous perennial habit. Specimens from arctic locations are very uniform in habit, closely resembling the type of the species. At the same time, they show notable variations in leaf shape (cf. vars. *flaccida*, *dentata*, *lyrata* Ledeb., R: 838) and especially in shape of the achenes, particularly in the degree of attenuateness at the summit (cf. fig. 154). Some of these differences in achene shape are doubtless genetic, but as the range of variation in this feature is continuous, the plants with very shortly beaked achenes are not recognized in the present treatment, even as numbered variants.

From the alpine and subalpine stations of more southerly latitudes come specimens showing a general trend toward larger size, especially in the leaves and heads, and occasionally a tendency toward elongated stems and branches (cf. var. *caulescens* Rupr. in B. Fedtschenko, *loc. cit.*). No doubt some of these variations are purely ecological (see, for example, m.v. 3). Even among the arctic plants a few variations of this sort occur, which, because they appear so different from the type, are noted below as m.v. 1. But the more extreme variations in size and habit from the mountains of W. North America very probably are genetic in nature. At least those noted below as m.v. 2, 3, and 4 are intergrades which connect the type form with certain definitely elongated ramose forms which diverge so widely from the type of the species as to make it necessary to recognize them as comprising a subspecies.

Key to the Subspecies of *Crepis nana*

- Plant tufted; stems not leafy; heads borne among the leaves; achenes about 0.5 mm wide, ribs narrower 107, *a. typica*
 Plant taller, the branches elongated; stems leafy; heads borne well above the basal leaves; achenes 0.5-0.7 mm wide, ribs broader 107, *b. ramosa*

107, *a. Crepis nana typica* subsp. nov. Planta humilis 0.2-0.7 dm. alta; inflorescentia aggregata congesta; folia caudicalia interdum 7 cm longa 1.5 cm lata; involucria 10-13 mm longa; corolla 7-8.5 mm longa; achaenia 4-8 mm longa 0.5 mm lata, costis angustis.

Plant tufted, 0.2-0.7 dm high, 4-12 cm wide; caudex slender, 1-4 cm long, much branched, branches congested, slender, 2-4-headed; caudical leaves up to 7 cm long, 1.5 cm wide; involucre 10-13 mm long; corolla 7-8.5 mm long; ligule 1.25-1.5 mm wide, teeth 0.3-0.5 mm long; corolla tube 2.5-4 mm long, slender, glabrous; anther tube (2.25) 2.5 × 0.75 (1) mm dis.; appendages 0.8 mm long, narrow, acuminate; filaments 0.5-0.75 mm longer; style branches about 1 mm long, 0.1 mm wide,

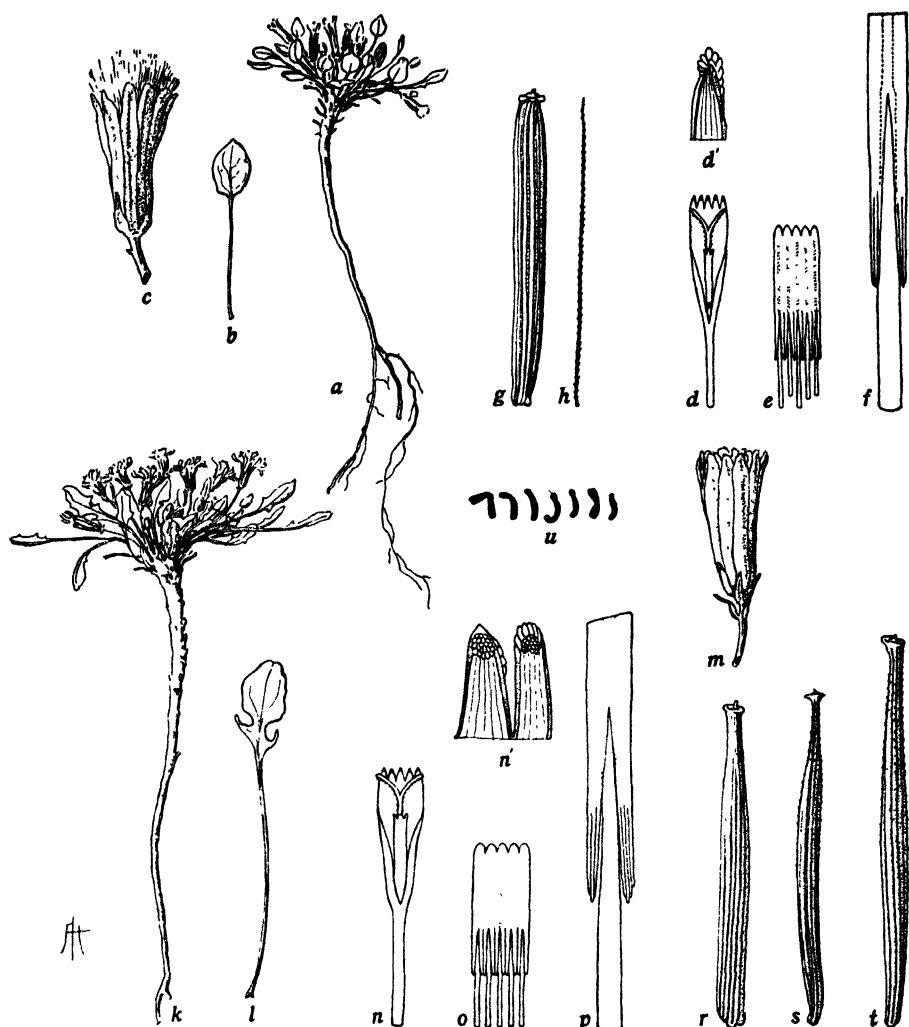


Fig. 154. *Crepis nana typica*, a–p, from type (K); r, from herb. Bunge (G); s, from herb. Hooker (K); t, from *Onion* in 1861 (NY); u, from hort. genet. Calif. 2698 (grown from seeds sent from Alaska by Professor G. W. Gasser): a, middle plant on type sheet, $\times \frac{1}{2}$; b, leaf from same, $\times 1$; c, head from same, $\times 2$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, h, achene and pappus seta, $\times 8$; i, j, detail of appendages, $\times 32$; k, right-hand plant on type sheet, $\times \frac{1}{2}$; l, leaf from same, $\times 1$; m, head from same, $\times 2$; n, floret lacking ovary, $\times 4$; o, anther tube, $\times 8$; p, detail of appendages, $\times 32$; q–t, achenes, $\times 8$; u, somatic chromosomes, $n = 7$, $\times 1250$.

obtuse, yellow; achenes 4–6 (8) mm long, 0.5 mm wide; pappus 4–6 mm long. Chromosomes, $2n = 14$. See fig. 154.

Prenanthes pygmaea Ledeb., Mem. Acad. Petersb. V ser., 5: 553. 1815.

Prenanthes polymorpha Ledeb., vars. a et b, Fl. Alt. 4: 144. 1833.

Barkhausia nano DC., Prod. 7: 156. 1838.

Youngia pygmaea var. a, Ledeb., Fl. Ros. 2: 838. 1844–1846.

Crepis humilis Fisch., ex Herder, Bull. Soc. Nat. Mosc. 43(1): 190. 1870.

Hieracioides nanum O. Kuntze, Gen. 1: 346. 1891.

Youngia nana Rydb., Fl. Rocky Mts. 1021. 1917.

Range of the species.

India: Kashmir, E. Ladak, Mepalungpa, *De Terra and Hutchinson 155 (169)* (NY). **Mongolia:** Altai reg., ex Herb. Bunge, 1839 (B, G, CP, Mo); Altai Mts., *Littledale* in 1897 (K); **Lake**

Kossogol, *Turczaninow* in 1836 (DC, K). **Siberia:** Irkutsk, Burjata-Mongolia border, Tunea dist., Oka R., near Boin-Nol, *Nazarov 15032* (Mosc); Yakutsk, Kumach-Sur, *Nilsson* in 1898 (US) m.v. 7; Kamchatka reg., between Alach-Jan and Okhotsk, *Turczaninow* ? in 1835 (DC, K); "Kamchatka or N.W. America," *Steller* (L).

Alaska: Port Clarence, *Kjellman* in 1897 (K); Alaska Range, McKinley National Park, Savage R., *Meria 2033* (UC); Alaska Range, Healy, *Anderson 1973* (NY) m.v. 1; Yukon Valley, Coal Creek Hill, *Funston 142* (G) m.v. 1; Porcupine R., *Turner* in 1891 (UC); Old Crow R., *Muris* in 1926 (UC) m.v. 1. **Canada:** Yukon, Dawson, bluffs along Klondyke R., *Eastwood 346* (UC) m.v. 1; Mackenzie R., *Onion et al.* in 1861-1862 (NY) m.v. 1; Arctic sea coast, "on Coppermine R.," *Richardson 378-80* (K) type, photograph (UC); *ibid.* (?) annotated "Hooker misit 1834-1835" (G, Fl) isotypes (?); Arctic coast, Ogden Bay to Coppermine R., *Hanbury* in 1902 (K). **Labrador:** Ramah, *Stecker 324* (G, UC, Minn, Wy); Okkak, *Weis* (K). **Newfoundland:** Pistolet Bay, Burnt Cape, dry limestone barrens, *Fernald et al. 29278* (Co). **Quebec:** Gaspé Pen., *vide* Fernald (Mem. Gray Herb. Harv. Univ. 2: 252, 1925). **British Columbia:** Kicking Horse Lake, *Macoun* in 1885 (G, CP, UC); Rocky Mts., Jasper House, *Hooker* in 1845 (K) m.v. 2; Rocky Mts., summit, *Lyall* in 1861 (K, G) m.v. 1. **Montana:** Rocky Mts., Marias Pass, *Canby 211* (K, CP, G) m.v. 2; Stanton Lake, *Williams* (Wy); Glacier National Park, Grinnell Glacier, *McKelvey* in 1921 (K). **Wyoming:** northwestern, *Parry* in 1873 (G). **Colorado:** Gray's Peak, headwaters of Clear Cr., *Patterson* in 1885 (K, FM); Fremont Co., Sierra Sangre de Cristo, *Brandege 894* (G) m.v. 2; Castle Peak, near Aspen, *Penland* in 1929 (UC). **Utah:** Beaver Co., Tushar (Belknap) Pk., E. slopes of peak and saddle, 3508-3660 m, loose calcareous talus, *Maguire 19784* (UC); Lasal Mts., Mt. Mellenthin, S.W. slope, 3720 m, *Maguire 21265* (UC); Gold Mt., *Jones* in 1901 (UC, Po) m.v. 3; between Alta and American Fork, *Leonard* in 1883 (Po) m.v. 3. **Nevada:** Lander Co., Toiyabe Range, Bunker Hill, *Kennedy 4196* (UC, DS) m.v. 3; Clark Co., Charleston Peak, above timber line, *Clokey 5639* (Clo). **Oregon:** Wallowa Mts., *Cusick* in 1900 (Po) m.v. 3. **California:** Sierra Nevada, Sonora Pass, *Brewer 1884* (G, UC) m.v. 3; Sierra Nevada, Tuolumne Co., near Leavitt Peak, *Sharsmith 2879* (UC) m.v. 3; Tuolumne-Mono counties, near Leavitt Peak, *Sharsmith 2893* (UC); Fresno Co., Mt. Gould, S. slope, coarse granite sand, *Sharsmith 3226* (UC); San Bernardino Range, Mt. San Antonio, E. side, near small snow field, *Burlew* in 1916 (UC).

Minor Variants of *C. nana typica*

1. Caudex and branches somewhat elongated. Probably ecads caused by submergence or partial covering with detritus. *Anderson 1973* (NY) Healy, Alaska Range; *Funston 142* (G) Coal Creek Hill, Yukon Valley, Alaska; *Muris* in 1926 (UC) Old Crow R., tributary of Porcupine R., Alaska; *Eastwood 346* (UC) Klondyke R., Dawson, Yukon, Canada; *Onion et al.* in 1861 (NY) Mackenzie R., Canada; *Lyall* in 1861 (K, G) summit of Rocky Mts., British Columbia (?).

2. Plant somewhat larger, especially the heads and achenes; involucre up to 13 mm long; achenes up to 8 mm long in some specimens, ribs prominent. *Hooker* in 1845 (K) Jasper House, Burke, Rocky Mts., British Columbia (?); *Canby 211* in 1883 (K, G) upper Marias Pass, Rocky Mts., Montana; *Brandege 894* (G) and *Brandege 924* (FM) alpine summits, Sierra Sangre de Cristo, Fremont Co., Colorado.

3. Leaves broader, both blade and petiole, and caudex somewhat elongated. *Jones* in 1901 (UC, Po) Gold Mt., Utah; *Leonard* in 1883 (Po) ridge between Alta and American Fork, Utah; *Kennedy 4196* (UC, DS) Bunker Hill, Toiyabe Range, Lander Co., Nevada; *Cusick* in 1900 (Po) sliding gravel, Wallowa Mts., Oregon; *Brewer 1884* (G, UC) Sonora Pass, Sierra Nevada, California; *Sharsmith 2870* (UC) S.W. slope of divide leading to Leavitt Peak from Sonora Pass, loose lava loam, Tuolumne Co., California.

7. Branches elongated (probably from growing up through detritus), 1-2-headed; outer involucre bracts $\frac{1}{4}$ - $\frac{1}{2}$ as long as the inner; corolla 10-11 mm long; corolla tube 5 mm long; style branches 1.5 mm long; pappus 6 mm long. The specimen is fragmentary, consisting of 2 branches with flowers and fruits and a small plant with leaves only. Although the 2 branches appear to represent an extreme variant in the features noted above, yet the involucre, achenes, and notably the anther appendages are typical. Also, at the base of 1 of the branches there is a small withered leaf which is lyrate-pinnatifid with 1 pair of small lateral lobes as occasionally seen in this species. *Nilsson* in 1898 (US) Kumach-Sur, Yakutsk, Siberia.

107. *b. Crepis nana* *var. nana* subsp. nov. Planta 0.8-1.8 dm alta colonifera; caules tenues ramosi, ramis remotis; inflorescentia aggregata composita paniculata; folia caudicalia interdum 8.5 cm longa 2.5 cm lata integra vel dentata; folia caulina similia vel sessilia lanceolata acuta; involucre plerumque 12-13 mm longa; corolla 7.5-9 mm longa, ligula circa 4 mm longa 1.5 mm lata; antherae circa 2.5 mm



Fig. 155. *Crepis nana ramosa*, a-g, from Purpus 5202 (UC 91853) = m.v. 6; k-q, from type (UC 470750): a, plant, $\times \frac{1}{2}$; b, branch, $\times 1$; c, floret lacking ovary, $\times 4$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, g, achene and pappus seta, $\times 8$; k, plant, $\times \frac{1}{2}$; l, branch, $\times 1$; m, floret lacking ovary, $\times 4$; n, anther tube, $\times 8$; o, detail of appendages, $\times 32$; p, q, achene and pappus seta, $\times 8$.

longae; rami styli 0.8–1.1 mm longi flavi; achaenia circa 6.5 mm longa 0.5–0.7 mm lata 10–13-costata, costis prominentibus; pappus 5–6 mm longus.

Plant with elongated stem and branches, 0.8–1.8 dm high, forming clumps from stolons; stems slender, terete, striate, often purplish, not fistulose, paniculately branched, branches remote, rebranched, the aggregate inflorescence an open or congested compound panicle; caudical leaves up to 8.5 mm long, 2.5 mm wide, entire or dentate; cauline leaves similar or sessile, lanceolate, acute; involucre 12–13 mm long (8–10 mm in m.v. 6); corolla 7.5–9 mm long; ligule 1.5 mm wide, teeth 0.3–0.5 mm long; corolla tube 3.25–5 mm long, slender, glabrous; anther tube (2.25) 2.5 × 1 mm dis.; appendages 0.8–0.9 mm long, narrow, acuminate; filaments 0.5–0.75 mm longer; style branches 0.8–1.1 mm long, 0.1 mm wide, obtuse, yellow; achenes 4.5–7 mm long, 0.5–0.7 mm wide, 10–13-ribbed, ribs prominent, rounded, rugulose; pappus 4–6 mm long. See fig. 155.

The type of this subspecies simulates *Crepis elegans* in habit, and upon cursory examination might easily be mistaken for that species. The achenes, floral features, and stoloniferous habit are characteristic of *C. nana typica*; and variants 4, 5, and 6 are intergrades between the two subspecies. It may at first appear that these elongated ramose forms are hardly worthy of recognition as a subspecies, especially when it is realized that the type locality has an elevation of only 1818 m and is in a region of very heavy rainfall. It is believed by the author, however, that these are distinct genetic forms and that they are already well on the way toward differentiation into a species, results of experimental cultures of *C. nana typica* tending to support this view. When grown under favorable conditions in a greenhouse in Berkeley, plants of subsp. *typica*, from seeds collected in N.E. Alaska, were exactly typical, showing no tendency whatever to elongation of the stem or branches. The type of subsp. *ramosa* may therefore be assumed to be an ecospecies in the sense of Turesson, and variants 4 and 6 are probably similar but less extreme genetic types. The existence of a series of intergrading variants between the two subspecies is just what would be expected, if the type of subsp. *ramosa* represents the accumulated result of a large number of mutations by means of which subsp. *typica* has been transformed back again into an upright, elongated ramose plant similar to the one from which it doubtless developed during its gradual adaptation to arctic and alpine conditions.

British Columbia: Rocky Mts., Banff reg. (†), *Bourgeau* in 1858 (G) m.v. 4. **Idaho:** Blaine Co., Smoky Mts., *MacBride and Payson 3740* (G, RM) m.v. 4. **Oregon:** Wallowa Mts., Hurricane Cr., *Cusick 1419* (G, CP, Or) m.v. 4. **Washington:** Cascade Mts., Yakima Co., Mt. Adams, *Suksdorf 4147* (G, US, DS, Minn, FM) m.v. 4; Olympic Mts., Clallam Co., Mt. Angeles, talus slopes below cliffs, *Thompson 7398* (Mo, Blake, UC); Jefferson Co., in Marmot Pass, rock slides, 1525 m, *Thompson 9921* (UC); Jefferson Co., near Marmot Pass, talus, *Helmrich 361* (WSC); Iron Mt., near Marmot Pass, coarse talus, *Thompson 7943* (US, Mo, UC); above Lake Constance, talus slopes, *Thompson 7883* (type UC 470750, Mo, Blake, DS). **California:** Yosemite National Park, Koip Pass, *Blasdale* in 1931 (UC) m.v. 5; Sierra Nevada, Farewell Gap, *Purpus 5202* (K, G, UC, Po) m.v. 6; *ibid.*, Excelsior Peak, *Mason 11451* (UC) m.v. 6.

Minor Variants of *C. nana ramosa*

4. Branches subelongated; heads not greatly exceeding the leaves; peduncles short, as in m.v. 6. *Bourgeau* in 1858 (G) Banff reg. (†), Rocky Mts., British Columbia; *MacBride and Payson 3740* (G, Wy) Smoky Mts., Blaine Co., Idaho; *Suksdorf 4147* (G, FM) Mt. Adams, Yakima Co., Cascade Mts., Washington; *Cusick 1419* (G, CP, Or) bars of Hurricane Cr. and adjacent subalpine summits, Wallowa Mts., Oregon.

5. Stems numerous from stolons, leafy; leaves narrow, elongated; ligules without purple, except on teeth. This may correspond to *Prenanthes polymorpha* var. *flaccida* Ledeb., Fl. Alt. 4: 144, 1833. It may be merely an extreme ecad of subsp. *typica* caused by partial burial under detritus. *Blasdale* in 1931 (UC) Koip Pass, Yosemite National Park, Sierra Nevada, California.

6. Leaves more as in subsp. *typica*; heads shortly pedunculate, and mostly in small clusters at the ends of the branches (fig. 155, *a-g*). *Purpus 5202* (K, G, UC, Po) Farewell Gap, Sierra Nevada; *Mason 11451* (UC) Excelsior Peak, Sierra Nevada, California.

Relationship

Crepis nana is very closely related to *C. elegans*, of which it is probably the progenitor. Although the two cannot certainly be distinguished by presence or absence of the beak of the achenes, as Hooker thought, yet the achenes differ constantly in shape, those of *C. nana* being always more columnar and broader at the base; also, the ribs of *C. nana* are broader and merely faintly rugulose, whereas in *C. elegans* they are narrower and definitely spiculate. Furthermore, the stoloniferous habit so characteristic of *C. nana ramosa* is never seen in *C. elegans*. Differences in floral characters are noted under *C. elegans*. Another very closely related species is *C. lactea*, which has comparatively large light red florets and long anther tubes, with longer truncate appendages. The next nearest relatives are *C. flexuosa*, *C. naniforma*, *C. alaica*, and *C. corniculata*, which are very distinct in numerous characters.

108. *Crepis elegans* Hook.

Fl. Bor. Am. 1: 297. 1834. (Fig. 156.)

Glabrous perennial, 1.5–2.5 dm high and as broad or broader; caudex 4–6 mm wide, cylindric or conical, rugose or scaly, simple or 2–4-divided, tapering into a strong woody taproot; stems several or numerous, stiffly erect or semierect, terete, striate, dichotomously branched from the base upward, in older plants excessively branched, forming a dense obconical clump topped by a mass of flower heads; caudical leaves numerous, up to 6 cm long, 1.5 cm wide, spatulate, blade elliptic or ovate, acute, entire or coarsely dentate, constricted below into a narrow petiole equal to or longer than the blade with broader clasping base, glaucous and purplish; cauline leaves linear, acuminate, petiolate or sessile, uppermost bractlike; heads erect, small, 6–10-flowered; involucre cylindric, 8–10 mm high, 2–3 mm wide; outer bracts 7–8, very short, unequal, ovate or oblong-lanceolate, acute; inner bracts 8–10, equal, oblong, acute or obtuse, purple at apex, in 2 ranks, inner ones broadly scarious-margined, glabrous on inner face, becoming carinately spongy-thickened, ultimately reflexed; receptacle areolate, glabrous; corolla in marginal florets 8 mm long; ligule 1 mm wide; teeth 0.2–0.25 mm long; corolla tube 4 mm long, very slender, glabrous, epidermal cells with prominent transverse septa simulating minute protuberances; anther tube 2.75×0.6 mm dis.; appendages 1 mm long, very narrow, acuminate; filaments 0.75 mm longer; style branches 0.5 mm long, yellow; achenes golden brown, 5 mm long, very slender, fusiform, subterete or definitely flattened on one side, attenuate into a delicate beak $\frac{1}{4}$ as long as body, with expanded pappus disk, attenuate or constricted to the very narrow calloused base, 10-ribbed, ribs narrow, spiculate; pappus white, 4 mm long, 1-seriate, very fine, soft, caducous. Flowering June–Sept.; flowers yellow. Chromosomes, $2n = 14$.

Barkhausia elegans Nutt., Trans. Am. Philos. Soc. 7: 485. 1841.

Hieraciodes elegans O. Kuntze, Gen. 1: 346. 1891.

Youngia elegans Rydb., Fl. Rocky Mts. 1021. 1917.

North America, from central Alaska south to Alberta, Saskatchewan, Montana, and Wyoming; along river banks, on sand bars, occasionally on dry plains and bluffs, 600–1500 m alt.

Monomorphic.

Alaska: Alaska Range, McKinley National Park, near middle of N. boundary, Moose Cr., sandy bar, *Mexia 2171* (UC); Alaska, Lynn Canal reg., in sand, *Krause 436* (B). **Canada:**

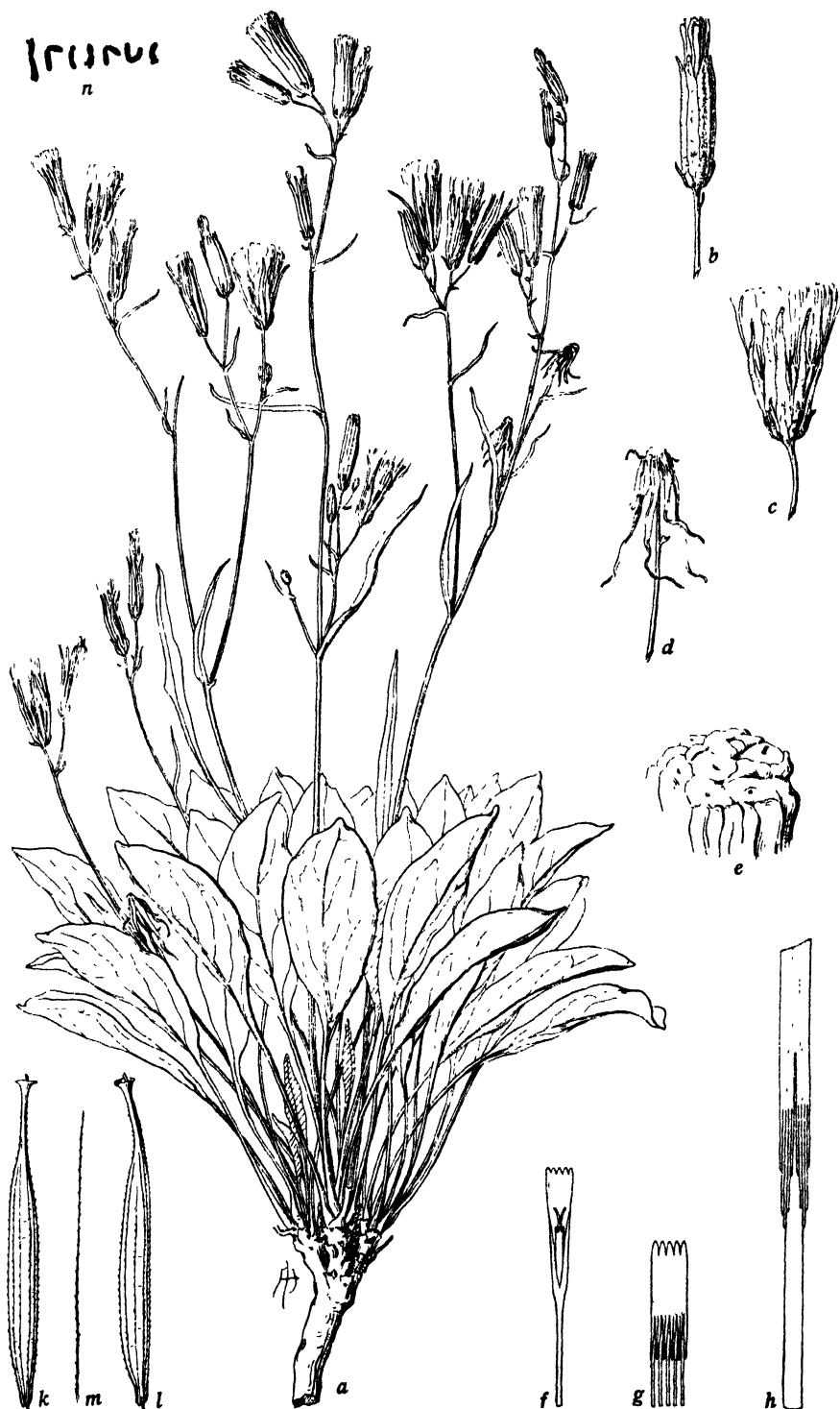


Fig. 156. *Crepis elegans*, a-m, from Canby 163 (UC 91854); n, from hort. genet. Calif. 2654 (grown from seeds collected in McKinley Park, Alaska, by Mrs. I. Mexia; cf. UC 353959): a, plant, $\times 1$; b, flowering head after anthesis, $\times 2$; c, mature head, $\times 2$; d, old head with reflexed bracts, $\times 2$; e, detail of receptacle, $\times 25$; f, floret lacking ovary, $\times 4$; g, anther tube, $\times 8$; h, detail of appendages, $\times 32$; k-m, 2 achenes and a pappus seta, $\times 8$; n, somatic chromosomes, $n = 7$, $\times 1250$.

Yukon, Dawson, bluffs along Klondyke R., *Eastwood* 346 (G, CA); Alberta, Rocky Mts., "battures of the Assiniboine river," *Drummond* (K) type, photograph (UCf), regarding the river named in the original description, Macoun (Geol. Surv. Canada, 1: 274, 1883) states: "This must be a misprint for battures of the Athabasca since the former river has no 'battures' (gravel beds extending into the river) while the latter has, near Jasper House, where Drummond was collecting"; Alberta, "Assiniboine river," *Drummond* (G) isotype; Alberta, headwaters of the Saskatchewan and Athabasca rivers, N. Saskatchewan R., "Kootany Plains," *Brown* 1489 (G); Alberta, Banff, *Canby* 163 (G, UC); Alberta, Banff Alta, Devil's Lake, *Butters et al.* in 1907 (G); Saskatchewan, *Bourgeau* in 1857-1858 (G); Saskatchewan, wasteland, *Bourgeau* in 1858 (K); British Columbia, Omeneca R., 64.5 km north of Takla Landing, *McCabe* 8031 (UC). U. S. A.: Montana, Glacier National Park, below Lake McDermott, sand bar along Swiftcurrent Cr., *Standley* 15918 (G); Lewis and Clark Co., 32 km west of Cadotts Pass, *Canby* in 1883 (K, G); Wyoming, Lincoln Co., Wind River Mts., *Nelson* 3614 (RM); Teton Forest Reservation, *Brandegee* in 1897 (UC).

Although very closely related to *Crepis nana*, and probably derived from it, *C. elegans* is very distinct in habit, flower parts and achenes. Also, its distribution in a warmer life zone sets it off sharply from *C. nana* and *C. flexuosa* as well as from the other higher altitude species of this section. At the same time, its similarity to *C. nana* is further indicated by its frequent occurrence on stream banks and sand bars. That it is a more advanced species than *C. nana* is indicated by the very narrow corolla and definitely beaked achenes, as well as its different ecological relations.

SECTION 13. INTYBELLIA

The 3 species comprising this section are characterized by a short praemorse rhizome, oblanceolate or obovate lower leaves and bractlike upper leaves, a slender stem with short branches near the top, forming a racemiform or subcorymbiform cymose inflorescence, medium or small heads, numerous involucre bracts, the longest outer bracts $\frac{1}{3}$ – $\frac{2}{3}$ as long as the inner, and the inner bracts becoming carinate

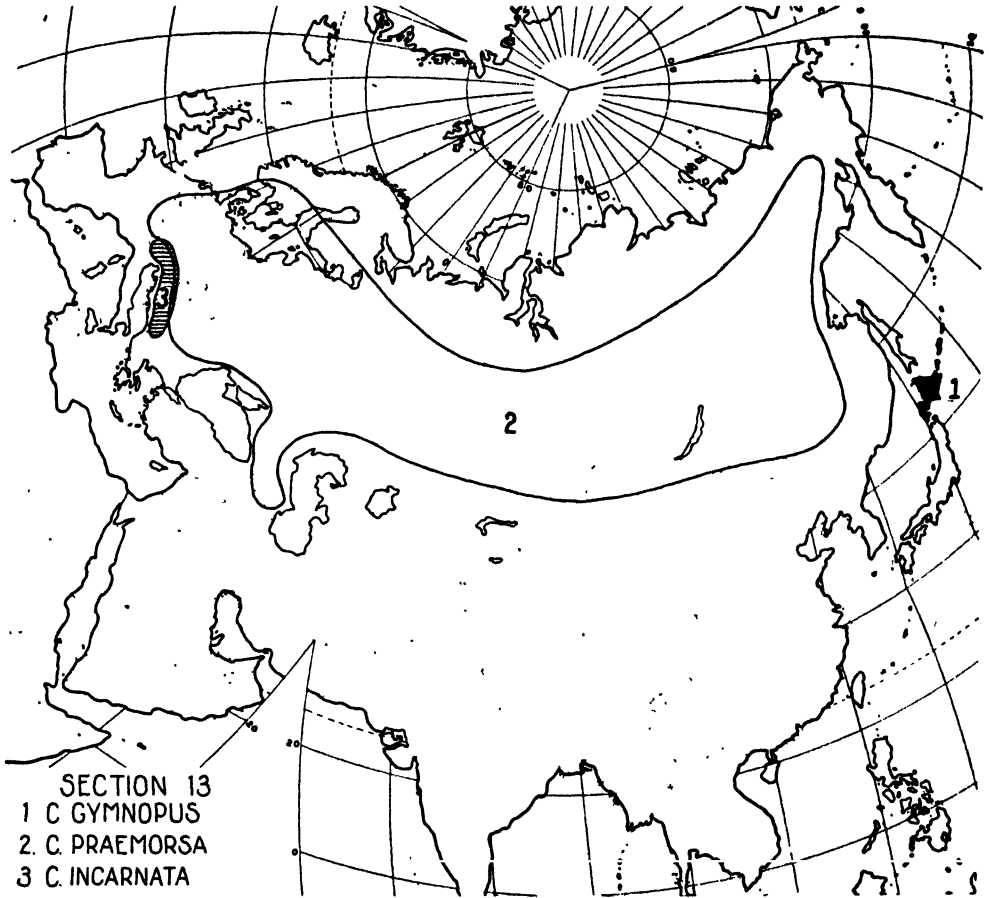


Fig. 157. Geographic distribution of the 3 species in sec. 13. Based on Goode Base Map No. 201 PC. By permission of the University of Chicago Press.

and spongy-thickened, beakless achenes with about 20 narrow ribs, and white pappus. The 3 species are very close, but *C. gymnopus* is more primitive than *C. praemorsa* and *C. incarnata*, on the basis of its larger florets, more broadly based achenes, and multiseriate pappus. *C. gymnopus* is endemic in the island of Hokkaido, Japan, and occurs on serpentine formations at elevations of from 1000 to 2000 meters. *C. praemorsa* is next in degree of primitiveness, as indicated by larger size of the plant and leaves, the shape and ribbing of the achenes, and the yellow flower color. It is distributed from the Atlantic to the Pacific across middle Europe and S. Siberia. It occurs on moist or rather dry alluvial soils in valleys, plains, and lower mountains. *C. incarnata* is much more variable than the other two species. That it is also more advanced is shown by the narrower achenes and often shorter

pappus, as well as by the pink flower color which typifies this species. All 3 species are diploids, and their karyotypes are very similar. Their geographic distribution (fig. 157) strongly indicates N. Central Asia as the region of origin for the section.

Key to the Species of Section 13

Leaves with the petiole about equal to the blade; corolla about 15 mm long. Japan 109. *C. gymnopus*, p. 549

Leaves with the petiole very short; corolla 9–12 mm long.

Leaves mostly oblanceolate and larger, 5–20 cm long, 1.5–5.5 cm wide; flowers yellow; anther appendages 0.5 mm long. Middle Europe and S. Siberia 110. *C. praemorsa*, p. 550

Leaves mostly obovate and smaller, 1.5–10 cm long, 0.8–2.8 cm wide; flowers pink, or, if yellow (m.v. 1), then restricted to S. Tirol, where *C. praemorsa* does not occur; anther appendages 0.8 mm long. S. central Europe 111. *C. incarnata*, p. 554

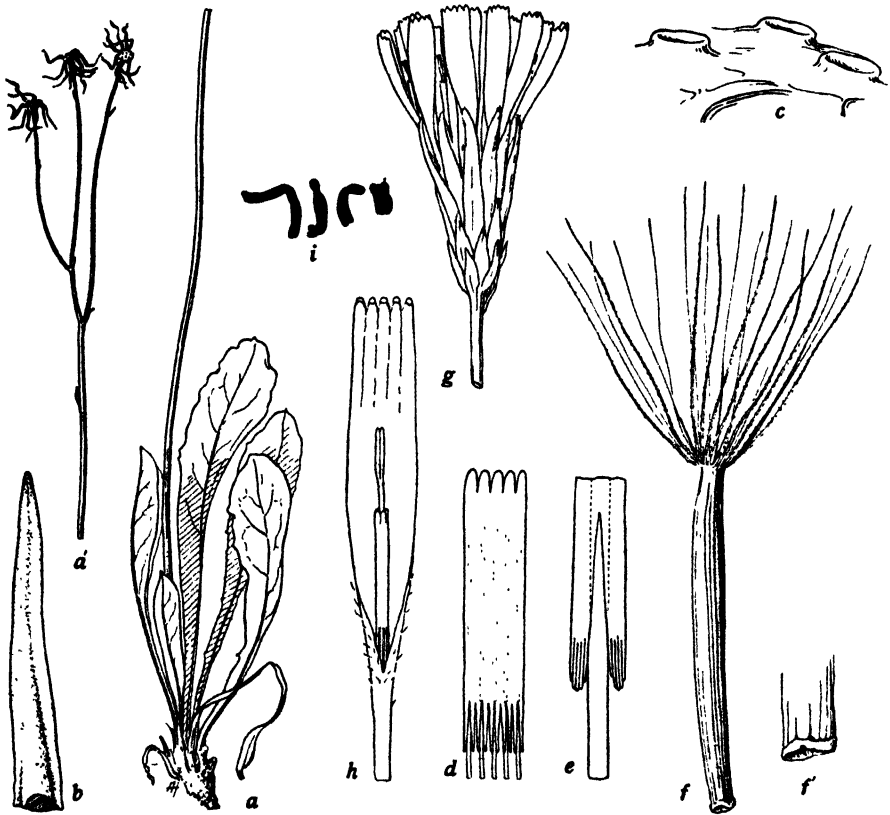


Fig. 158. *Crepis gymnopus*, a–f, from isotype (UC 346585); g, h, from Tatewaki in 1927 (UC 346440); i, from hort. genet. Calif. 2746 (grown from seeds collected in Hokkaido; cf. UC 429494): a, plant, $\times \frac{1}{2}$; b, inner involucre bract, $\times 4$; c, detail of receptacle, $\times 25$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, achene and pappus, $\times 8$; f', base of achene, $\times 16$; g, flower head, $\times 2$; h, floret lacking ovary, $\times 4$; i, somatic chromosomes, $n = 4$, $\times 1250$.

109. *Crepis gymnopus* Koidzumi

Tokio Bot. Mag. 31: 141. 1917. (Fig. 158.)

Perennial, 3–4.5 dm high; rhizome 1–3.5 mm long, vertical or oblique, slender, praemorse, fibrillate, swollen at crown; caudex short, 0.5–1 cm wide, covered with brown bases of old leaves; leaves all caudical (except small linear bracts at bifurca-

tions of the inflorescence), 3–13 cm long, 0.7–3.3 cm wide, spatulate, blade broadly to narrowly elliptic or obovate, obtuse or acute, remotely repand-denticulate, teeth mucronate, margin revolute, abruptly or gradually attenuate into a narrowly winged petiole about equal to the blade, puberulent on upper face with short whitish hairs or glabrescent; stem erect, slender, terete, striate, glabrous, cymosely few-branched near summit, forming a 3–8-headed cymose corymbiform inflorescence; peduncles 1–7 cm long, erect, slender, glabrous, somewhat thickened near head in fruit; heads erect, small, 10–15-flowered; involucre cylindric, 10–11 mm long, 3–4 mm wide at middle in fruit, glabrous; outer bracts 10–14, imbricate, unequal, longest about $\frac{1}{3}$ as long as the inner in fruiting heads, deltoid to lanceolate, acute, ciliate at margin; inner bracts 12–14, lanceolate, acute, ciliate at apex, glabrous on both sides, becoming broadly carinate, scarious and pale spongy-thickened confluent with the base in fruit; receptacle punctate, naked; corolla about 15 mm long; ligule 1.5–2 mm wide; teeth 0.2 mm long; corolla tube about 4 mm long, densely pubescent near base of ligule with fine short acicular hairs; anther tube (4) 4.5×1 mm dis.; appendages 0.8 mm long, oblong, narrow, acute; filaments about 0.5 mm longer; style branches about 1 mm long, 0.2 mm wide, yellow; achenes light brown, 4.5–5.5 mm long, 0.6–0.7 mm wide, fusiform, more strongly attenuate to the summit, with expanded pappus disk, lightly calloused at the pale rather broad hollow base, about 20-ribbed, ribs very narrow, rounded, smooth, nearly equal or alternate ribs weaker; pappus white, 5–6 mm long, 3–4-seriate, setae numerous, very fine, coarsest 20–30 μ wide at base, soft, persistent. Flowering May–June; flowers yellow. Chromosomes, $2n = 8$.

Northern, central, and southern Yezo (Hokkaido), Japan; mountains from approximately 1000 to 2000 m elevation; on serpentine formation; endemic.

Monomorphic.

Japan: Yezo (Hokkaido), Mt. Yubarisán, alpine belt, *Koidzumi* (Tokio, type; UC 346585 isotype); Hokkaido, Prov. Ishikari, Mt. Yubari, *Ishida* in 1928 (UC); *ibid.*, on serpentine rocks, *Takeda and Tatewaki* in 1921 (UC); N. Hokkaido, Prov. Teshio, along the Nupurumapporo, a branch of the Teshio R., in serpentine rock reg., *Tatewaki* in 1927 (UC); S. Hokkaido, Prov. Hidaka, near Cape Erimo, Mt. Apoi, serpentine rock reg., *Tatewaki* in 1927 (UC).

Relationship

Crepis gymnopus exhibits strong resemblance to the two following species in rhizome, leaf shape, habit of inflorescence, flowers, and fruits. It may be considered more primitive than either of them on the basis of the larger florets, the slightly larger achenes with a broader base, and the multiseriate pappus. It is less close to *C. runcinata glauca*, with which it was compared by *Koidzumi (loc. cit.)*, even though it may represent one of the original stocks that entered, through hybridization, into the ancestry of *C. runcinata*.

110. *Crepis praemorsa* (L.) Tausch

Flora 11 (I. Erg.): 79. 1828. (Fig. 159.)

Perennial, 1.5–7.5 (mostly 2.5–5.5) dm high; rhizome 1–3 cm long, slender, praemorse, fibrillate; caudex short, 0.5–1 cm wide; leaves all caudal, except small bracts at bifurcations of inflorescence, or rarely 1 cauline leaf near middle, subtending a small branch (unusually robust specimens), 5–20 cm long, 1.5–5.5 cm wide, mostly oblanceolate, or oblong, elliptic, or lanceolate, obtuse, acute or apiculate, entire or obscurely denticulate to repand-dentate, margin narrowly revolute, abruptly or gradually contracted into the winged petiole, densely pubescent with very short pale hairs or glabrescent; stem erect, stout or slender, terete, fistulose,

striate, densely and finely pubescent or glabrous, racemosely branched near summit, branches short, pedunculate or 2–3-headed, or rarely the lower branches elongated, with up to 6 heads, forming a racemiform or pyramidal simple or compound cyme; peduncles 1–2.5 cm long, slender, canescent-tomentose or scabridulous; heads erect, medium, 25–30-flowered; involucre cylindric, 8–12 mm high, 4–5 mm wide at middle in fruit, dark or pale green, pubescent with pale glandless hairs or glabrescent; outer bracts 8–12, imbricate, longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner, lanceolate, acute or obtuse, often ciliate at margin; inner bracts 12–18, narrow, lanceolate, acute or acuminate, white-ciliate at apex, glabrous on inner face, becoming narrowly carinate dorsally and pale spongy-thickened near base in fruit; receptacle punctate, glabrous; corolla 11–12 mm long; ligule about 1.75 mm wide; teeth 0.2–0.4 mm long; corolla tube 3.75–4 mm long, densely pubescent with short several-celled acicular hairs; anther tube about 3.75×1 mm dis.; appendages about 0.5 mm long, oblong, acute; filaments 0.75 mm longer; style branches 1.25 mm long, 0.1 mm wide, yellow; achenes light brown (olive green when immature), paler at apex and base, about 4 mm long, 0.6–0.7 mm wide, subterete or subcompressed, fusiform, about equally attenuate to both ends, with slightly expanded pappus disk, thinly calloused at the somewhat flaring hollow base, about 20-ribbed, ribs narrow, irregularly unequal, rounded, smooth; pappus white, 4.5–5 mm long, 2-seriate, setae very fine, coarsest about 30μ wide at base, soft, deciduous. Flowering Apr.–June; flowers yellow. Chromosomes, $2n = 8$.

Hieracium praemorsum L., Sp. Pl. 801. 1753, non All.

H. spicatum Gilib., Fl. Lithuan. 3: 238. 1781–1782.

Geracium praemorsum Rehb., ex Moessl., Handb. ed. 2, 2: 1367. 1827–1829.

Intybus praemorsus Fries, Nov. Pl. Suec. ed. 2: 245. 1828.

Intybellia praemorsa Monn., Essai Hierac. 79. 1829.

H. lactuaceum Schrank., ex DC., Prod. 7: 164. 1838.

Crepis fistula Fisch., ex Besser, in Ledeb., Fl. Ros. 2: 825. 1844–1846.

C. racemosa et *racemiforme* Car. et St. Lag., Fl. Moy. Rhone et Loire 499. 1889.

Hieraciodes praemorsum O. Kuntze, Gen. 1: 346. 1891.

Europe, in S. Scandinavia, Finland, Denmark, Germany, E. France, Switzerland, N. Italy, Austria, Hungary, Czechoslovakia, Rumania, the N. Balkan states (where it is rare), across Russia to the Urals and from the Caucasus to Leningrad; Asia, in middle and S. Siberia, as far east as Yakutsk and Manchuria, acc. to Ledebour (*loc. cit.*). Reported from the Altai Mts. by Keller (In Berg und Thal des Altai, 1: 39, 45, 51, 66. 1914).

Acc. to Hegi (1158), this species forms close stands in rather dry infertile fields, along margins of woods and thickets, in open forests and clearings, on plains and lower montane regions from 925 to 1200 m alt. Braun-Blanquet and Rübel (1483) report it from 500 to 1350 m in the middle E. Swiss Alps. *C. praemorsa* is considered by Hegi as one of the noteworthy plants of the middle European flora. On the basis of its total area, it is placed as intermediate between the Pontosarmatic-central European and the Sarmatic-central European type of distribution, even though it occurs mainly at the lower elevations of montane regions. Lest too much emphasis be placed on the xerophytic connotation of its Sarmatic association, however, it should be noted that (acc. to Hegi, *loc. cit.*) Braun-Blanquet reports that this species is characteristic of the marshy meadows of the Rhein Valley, where it occurs in groups on the moist, oozy alluvium near *Orchis militaris*, *O. ustulatus*, *Primula farinosa*, and *Scorzonera humilis*. Acc. to Braun-Blanquet and Rübel (*loc. cit.*), in the middle E. Swiss Alps it occurs only in the Rhein Valley and mostly on clayey soils in marshes and seldom in turf in open deciduous woods and borders of forests. Evidently it is a moisture-loving plant; but it is

equally evident that this species readily adapts itself to drier situations. It is quite possible that physiological ectotypes exist, which differ in their optimum degree of soil moisture; but it is highly probable that this species originated in a moist habitat. Besides a certain degree of warmth, it also requires an open subsoil and a not too sunny exposure. Its wide distribution is probably correlated with its varied soil

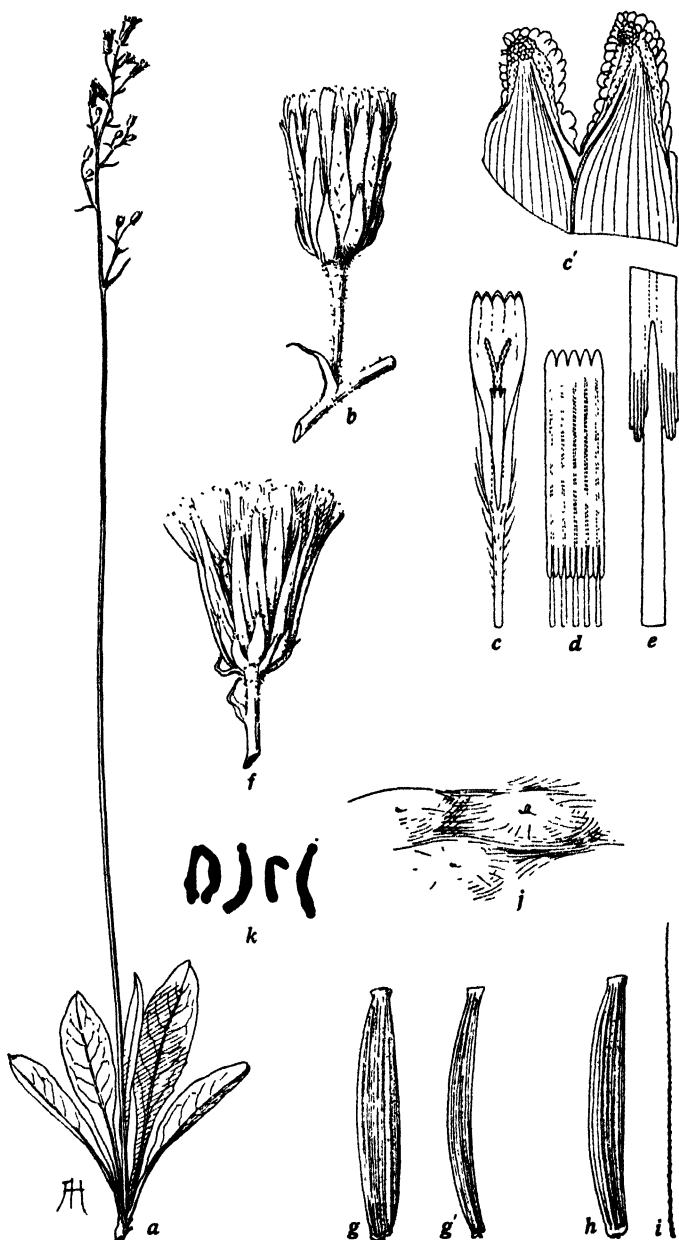


Fig. 159. *Crepis praemorsa*, a-e, from Callier, *Fl. silesiaca* exs. 216 (UC 669401); f-j, from hort. genet. Calif. 28.2133-2 (UC 669367); k, from hort. genet. Calif. 2133 (grown from seeds collected near Moscow by Dr. M. Navashin): a, plant, $\times \frac{1}{4}$; b, head before anthesis, $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule teeth, $\times 50$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, fruiting head, $\times 2$; g, g', marginal achene, $\times 8$; h, i, inner achene and pappus seta, $\times 8$; j, detail of receptacle, $\times 25$; k, somatic chromosomes, $n = 4$, $\times 1250$.

relations which Drude (322) indicates by his observation that, in S.W. Germany, it occurs on the boundaries between calcareous and basaltic formations. Further details of local distribution and associations in Europe are given in Hegi (1158–1159).

Although considerable variation occurs in the length of the branches of the inflorescence and in the number of heads, the habit is always racemiform. Aside from these variations and a rather wide range in size of leaves and height of stem, this species is remarkably uniform in view of its very wide distributional area.

Monomorphic.

Locality unknown: (L) type. **Norway:** Nesøen, *Anderson* in 1906 (Mo); near Christiania, *Dyring* in 1888 (Minn). **Sweden:** Uppland, Uppsala, *Asplund* in 1929 (UC); Södermanland, Toir, *Asplund* in 1929 (Mo); Smot, Dref, *Hylten* in 1881 (US); Necke, *Bagenholm* in 1894 (Minn). **Denmark:** Janstrup Vars, *Wünstrott* in 1907 (US). **France:** Maxeville, *Petitmengin* in 1902–1903 (Ms, UC); Meuse, Bois de Bras, *Bullemont* in 1892 (Bur); Savoie, Col du Frêne, opposite Apremont, near Chambrey, *Songeon* in 1864 (Mo). **Switzerland:** Jura, near Basle, Ramsach, *Siegfried* in 1869 (DS); Jura, Neuchatelais, Chaumont, *Sire* in 1872 (Bur); no definite locality, *Koelle* (BW n. 14654–1). **Germany:** Mark, Koepenick, *Woller* in 1900 (Minn); Palatinate, near Deidesheim, *Schultz Bipontinus* (Mo); Bavaria, Windsheim, *Semler* in 1904 (Mo); Upper Bavaria, Steingaden, *Neth* in 1900 (Minn); Silesia, Breslau, Bischwitz, *Kionka* in 1890 (Bur, UC); Hunnendorf, Untersleinach, *Puchtl* in 1907 (Bur); Thuringia, *Prager 14200* (CA). **Austria-Hungary:** Vienna, Weidling, Rothgrabens, *Keller* in 1891 (UC); Upper Austria, Schwerthberg, *Keck* in 1874 (UC); Karlatina, Zuecina, *Stopsyner* in 1870 (Bur); Leitmeritz, Sadane, *Missbach* in 1911 (Bur); Budapest, *L.S.* in 1876 (DS). **Czechoslovakia:** Bohemia, near Prag, *Tausch* (PD) as *H. praemorsum*; Bohemia, Siebenbürgen, Monora, *Barth* in 1897 (Minn). **Rumania:** Transylvania, Cojocna, near Cluj, 550 m, *Nyarady* in 1925 (US, Mo). **Russia:** near Kaluga, *Litvinov* in 1894 (Bur); Prov. Tambow, *Schirajewsky* in 1907 (Bur). **Siberia:** Omsk Prov., near Omsk, *Evseenko* in 1930 (G); Tomsk Prov., *Kuznezow 72* (NY); Yeniseisk Prov., Krasnoyarsk dist., *Tugarinowa* in 1908 (UC).

Relationship

Crepis praemorsa is very close to *C. incarnata* and has been united with the latter by Fiori (441). But most European botanists have preferred to recognize the two as different species (cf. Bischoff, 244–329; Hegi, 1158; Markgraf, 855). The distinguishing characteristics of the 2 species are summarized under *C. incarnata*. These 2, together with *C. gymnopus*, comprise a closely related group; they are similar both in gross morphology and in their karyotypes.

The present wide distribution of *C. praemorsa*, from the Atlantic to the Pacific across middle Europe and Asia, and the fact that one closely related species is restricted to Japan and the other to S.-central Europe, suggest that *C. praemorsa* originated in Central Asia and migrated into Europe as far west as Scandinavia in preglacial times.

The numerous resemblances between *C. praemorsa* and *C. napifera* of sec. 17 should also be noted (see figs. 149 and 190). The most striking difference between the two is subterranean, *C. napifera* having a long woody root, and *C. praemorsa*, a short vertical rhizome. There is also considerable difference in size of the flower heads, and some difference in leaf shape and in degree of inequality in width of ribs on the achenes. But the resemblances are really striking and they include such minute details as the ligule teeth and the type of hairs on the corolla tube. Certainly there is sufficient similarity between the two species to indicate a common origin. This fact justifies the inclusion of *C. napifera* in this genus, and it is consistent with the hypothesis that *Crepis* originated in northern Central Asia (see Part I, chapters 5, 6, and 8).

111. *Crepis incarnata* (Wulf.) Tausch

Flora 11 (I. Erg.): 79. 1828. (Figs. 160, 161.)

Perennial, 0.8–6 (mostly 2–4) dm high; rhizome short, slender, praemorse, strongly fibrillate; caudex short, 0.3–0.8 cm wide; leaves all caudical, except small bracts at bifurcations of inflorescence, or rarely 1 cauline leaf near middle, subtending a branch (in more robust specimens), 1.5–10 cm long, 0.8–2.8 cm wide, mostly obovate, or elliptic, oblanceolate or lanceolate, obtuse, acute, or apiculate, entire or obscurely denticulate to repand-dentate, margin narrowly revolute, abruptly or gradually contracted into the winged petiole, densely pubescent with very short pale hairs or glabrescent; stem erect, slender, fistulose, striate, glabrose or puberulent near base, dichotomously or corymbosely or racemosely branched near the summit, the aggregate inflorescence a corymbiform or sometimes racemiform simple or compound cyme; peduncles 0.5–5 cm long, slender, canescent-tomentulose or tomentose near the head or glabrous; heads erect, small to medium, 12–48 (mostly 20–30)-flowered; involucre cylindric, 7–12 mm high, 3–5 mm wide at middle in fruit, dark or pale green, glabrous or canescent-tomentose at the base; outer bracts 8–18, imbricate, longest $\frac{1}{3}$ – $\frac{2}{3}$ as long as the inner, acute or sometimes obtuse, often pale-margined and ciliate at the apex; inner bracts 10–22, narrow, lanceolate, acute or acuminate, white-ciliate at apex, glabrous on inner face, becoming narrowly carinate dorsally and pale spongy-thickened near base in fruit; receptacle punctate, glabrous; corolla 9–12 mm long; ligule 1–1.75 mm wide; teeth 0.15–0.5 mm long; corolla tube 3–4.5 mm long, pubescent with several-celled acicular hairs; anther tube (3)4 × 1 mm dis.; appendages about 0.8 mm long, lanceolate, acuminate; filaments 0.75–1 mm longer; style branches 1–2 mm long, 0.1 mm wide, purple or yellow; achenes light brown, 4–5 mm long, 0.4–0.6 mm wide, subterete, more strongly attenuate upward, with expanded pappus disk, thinly calloused at the somewhat flaring hollow base, about 20-ribbed, ribs nearly equal or 3–4 stronger, rounded, smooth; pappus white, 3.5–5 mm long, 2-seriate, the setae very fine, coarsest about 30 μ wide at base, soft, deciduous. Flowering May–July; flowers pale rose, pale lilac or white, or, in m.v. 1, yellow. Chromosomes, $2n = 8$.

*Hieracium montanum*¹ Scop., Fl. Carn. ed. 2, 106. t. 50. 1772.

H. incarnatum Wulfen, ex Jacq., Coll. 2: 127. 1788; Ic. Rar. t. 578. 1786–1793.

Geracium parviflorum Rehb., ex Moessl., Handb. ed. 2, 2: 1367. 1827–1829.

G. incarnatum Rehb., ex Moessl., *op. cit.*, 1368.

Intybellia incarnata Cass., ex Monn., Essai Hierac. 79. 1829.

Crepis Froelichiana DC., Prod. 7: 165. 1838.

Hieracium parviflorum Schleicher, *H. auriculaefolium* Willd., et *C. auriculaefolia* Froel., non Sieb., ex DC., *loc. cit.*

C. parviflora (Rehb.) Kreutzer, Anthochron. Pl. Eur. Med. 27: 220. 1840.

C. dinarica Beck, Ann. Naturh. Hofmus. Wien 2: 169, t. 3, f. 2. 1887.

*Hieraciodes montanum*¹ O. Kuntze, Gen. 1: 345. 1891.

N.E. Italy, S.E. Switzerland, S. Austria, Tessin, Karnik and Julie Alps, Lombardy, Krain, and southward through Dalmatia and Bosnia to Montenegro. Acc. to Hegi (1160), this plant occurs on calcareous formations from 600 to 1800 m alt., and is found growing either singly or in small groups in meadows, at edges of forests, on grassy, stony slopes, and in forest clearings.

In connection with the distribution, it is to be noted that there are 2 flower-color forms which occur in overlapping areas and occasionally hybridize in nature. The typical form, with pale rose or lilac (sometimes white) flowers, occurs (acc. to Hegi,

¹ Scopoli's name is invalidated under Art. 61 of the International Rules of Nomenclature, Jour. Bot. Suppl. 1931; cf. *C. montana* Urv.

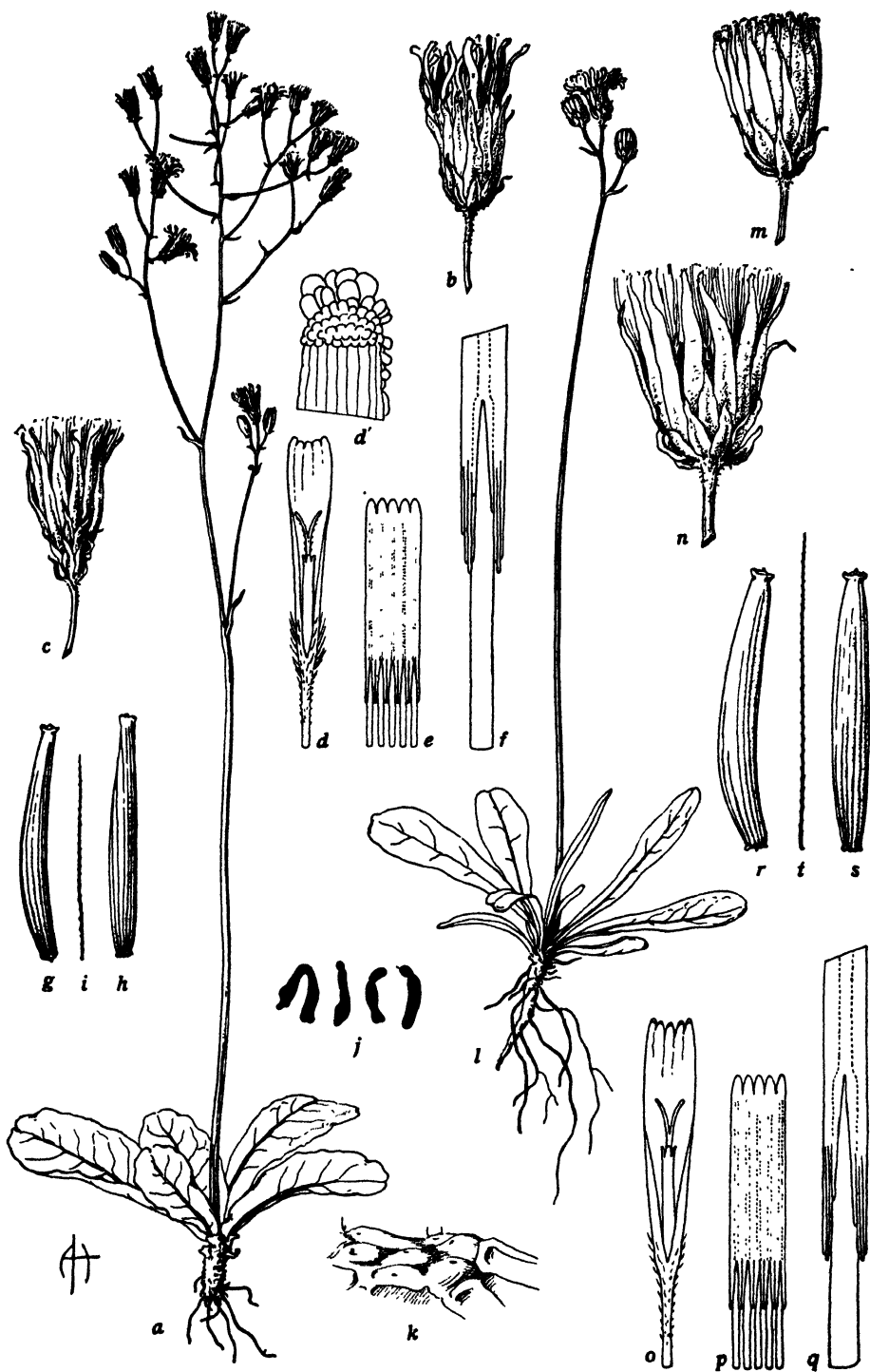


Fig. 160. *Crepis incarnata*, a-f, from Müller in 1904 (UC 160302); g-k, from hort, genet. Calif. 28.1304-2, 10 (UC 669372); l-t, from Curcio in 1898 (Po 10533): a, plant, $\times \frac{1}{2}$; b, flowering head, $\times 2$; c, mature head, $\times 2$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g-i, 2 achenes and a pappus seta, $\times 8$; j, somatic chromosomes, $n = 4$, $\times 1250$; k, detail of receptacle, $\times 25$; l, plant, $\times \frac{1}{2}$; m, immature head, $\times 2$; n, nearly mature head, $\times 2$; o, floret lacking ovary, $\times 4$; p, anther tube, $\times 8$; q, detail of appendages, $\times 32$; r-t, 2 achenes and a pappus seta, $\times 8$.

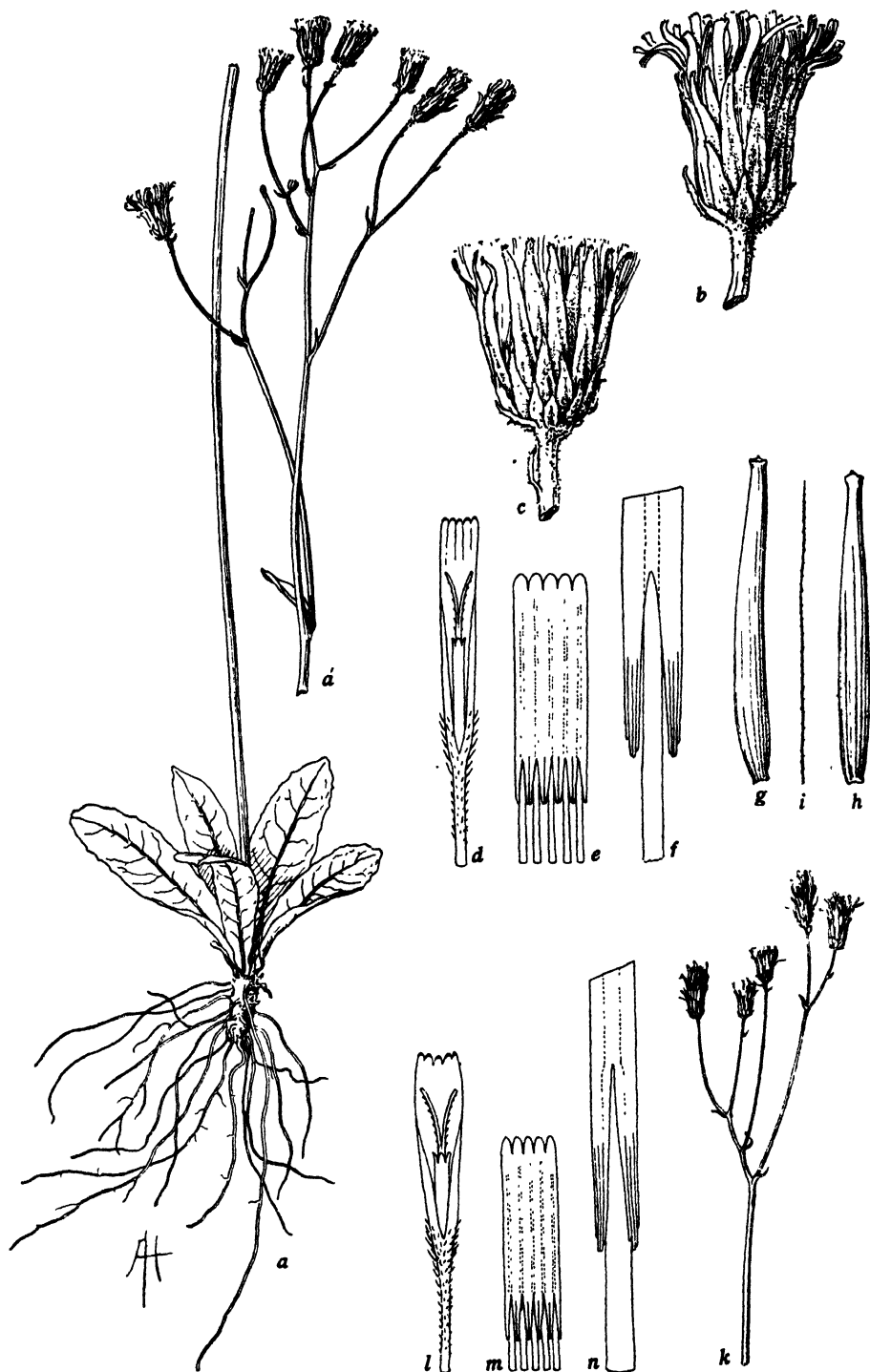


Fig. 161. *Crepis incarnata*, from Rigo in 1916 (UC 669512, as *C. Froelichiana* DC.): a, plant, $\times \frac{1}{2}$; b, flowering head, $\times 2$; c, mature head, $\times 2$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g-i, 2 achenes and a pappus seta, $\times 8$; k, upper part of another plant in same collection, $\times \frac{1}{2}$; l, floret from same, $\times 4$; m, anther tube, $\times 8$; n, detail of appendages, $\times 32$.

loc. cit.) in S. Tirol only east of the Etsch R., rather frequently in the Dolomites (and in adjacent mountain ranges), very often in the Karnic and Julie Alps, in the Karawanken Mts., and locally in Krain and Istria. I have also seen a number of specimens from Bosnia. The yellow-flowered form, on the other hand, seems to be restricted to the valley of the Etsch R. and closely adjacent regions to the west as well as the east, except for a few localities in Tessin, Switzerland, and over the border near Lake Como in Italy. In general, the yellow-flowered form has a more restricted western distribution, the pink-flowered form a wider eastern distribution, and the two overlap east of the Etsch R. in S. Tirol. Since, in the Compositae, yellow is generally considered a more primitive flower color than pink or white, an interesting question is raised concerning a possible physiological adaptation in attempting to explain the wider geographic distribution of the typical pink-flowered form. The specimens of the yellow-flowered form which I have seen will be cited separately under m.v. 1.

In both flower-color forms there is a remarkable range of variation in size of heads, number of involucre bracts, and number of florets per head, as compared with the range in *C. praemorsa* (cf. table 15). This raises a question whether polyploidy exists in *C. incarnata*. A thorough study has not been possible, but the following data on the pollen grains in the two species appear to have some significance. The largest and smallest *C. praemorsa* plants available (both from Germany) had flower heads closely similar in size, and both had regular, 3-pored pollen grains averaging about 30μ in diameter. Two pink-flowered plants of *C. incarnata* were examined. One, from N.E. Italy, had a single stem bearing 4 small heads containing 12–22 florets; and this plant had 3-pored pollen ranging from 30 to 37μ in diameter (average about 34μ). The other plant, from Bosnia, was similar in size, but it had 3 stems, each with 3 heads, the heads being much larger and with as many as 48 florets; this plant had 3-pored pollen ranging from 28 to 38μ in diameter (average about 34μ). From this evidence it appears that polyploidy is not involved in *C. incarnata*, but that it is inherently a much more variable species than *C. praemorsa*, and that this variability extends even to the size of the pollen grains.

Without definite locality: ex alpinus, *Tausch* (PD) type of *Tausch*; *ibid.*, Herb. Willd. n. 14656–2 (BW); *ibid.* (DC. Prod. vii. 165 n. 25), as *Hieracium incarnatum*. **Austria:** Kärnten, Arnoldstein, *Miller* in 1904 (UC); Kärnten, Mt. Selenitz, Loibl Valley, *Jabornegg* (Bur, G, Minn); Kärnten, Villacher Alps, Bleiberg, 900 m, *Schack* in 1926 (G). **Italy:** Tirol, Pustertal, Toblach, *Schwemer* in 1895 (Po); S. Tirol, northeast of Dolomites and Cadoric Alps, Schludersbach, *Sterneck* in 1901 (Po, Minn) with m.v. 1; S. Tirol, Cadoric Alps, ex hort. genet. Calif. 28.1304–13 (UC); middle Tirol, Alpe Aguerola, near Primiero, *Burnat* in 1873 (Bur); *ibid.*, Boudone au Tombea, *Burnat* in 1873 (Bur); Karat littoral, around Govitia, *Tommasini* (G); Udine Prov., Venetian Alps, Cortina (Giais), *Pease 1853* (G); Treviso Prov. near Narvesse (Narvesse ?), *Kellner* (G, Po); N.E. Italy, between the Karnic and Julie Alps, Seissera R. reg., *Kapu, Bens* in 1901 (UC). **Bosnia:** Treskavica, 1600 m, *Beck* in 1888 (UWH); *ibid.* 1900 m, *Fiala* in 1893 (US); near Sarajevo, Trebevic, *Curcic* in 1898 (Po); Travnil, Vlasie, 1200–1700 m, *Brandis* in 1895, 1903 (Bur, Po, UC).

Minor Variant of *C. incarnata*

1. (*C. Froelichiana* DC., *loc. cit.*; *Geracium parviflorum* Rehb., ex Moessl., *loc. cit.*; *Hieracium parviflorum* Schleicher, *H. auriculaefolium* Willd., et *C. auriculaefolia* Froel., ex DC., *loc. cit.*) (Fig. 161.) Ligules, anther tubes, and styles yellow; otherwise typical and apparently just about as variable in size of plant, leaves, and heads. The distribution, as compared with that of the typical form, is discussed above. Acc. to Hegi (*loc. cit.*), just south of the Pustertal, in the Enneberg dist., on the Armentara meadows, Handel-Mazzetti found many plants of this species having an intermediate flower color and representing, in all probability, a product of natural crossing. The following specimens of this form have been seen by me: *Muret* (Bur) San Salvador, Alpes de Cadro, Tessin, Switzerland; *Gysperger* in 1904 (UC) San Martino, near Cadenabbia, Lake Como, Italy; *Gelmi* in 1892 (Bur, US) Mt. Vasone, near Tridentum, Tridentina, Tirol,

Italy; *Halacsy* in 1894 (Bur) near Paneveggio, 1600–1900 m, S. Tirol, Italy; *Rigo* in 1904 (Bur) above Tour del Benaco, 150–200 m, Verona Prov., Italy; *Sterneck* in 1901 (Minn) Schluderbach, northeast of Dolomites and Cadoric Alps, S. Tirol, Italy; *Rigo* in 1873, 1883, 1916 (Mo, Po, UC) Verona reg., Venezia Prov., Italy; *Wolf* in 1896 (UC) Penegal, near Bozen, Mendel Mts., S. Tirol, Italy; *Rottenbach* in 1903 (UC) Bad-Ratzes, east of Bozen, S. Tirol, Italy.

TABLE 15

SYNOPTICAL COMPARISON OF THE MORPHOLOGICAL CHARACTERS AND DISTRIBUTIONAL FEATURES
DISTINGUISHING *CREPIS PRAEMORSA* FROM *C. INCARNATA*

Character	<i>C. praemorsa</i>	<i>C. incarnata</i>
Morphological comparison		
Plant, height.	1.5–7.5 dm	0.8–6 dm
Caudex, width	0.5–1 cm	0.3–0.8 cm
Leaf, size..	5 × 1.5 to 20 × 5.5 cm	1.5 × 0.8 to 10 × 2.8 cm
Leaf, shape.	mostly oblanceolate	mostly obovate
Stem, size. . . .	stout or slender	always slender
Stem, pubescence	dense or absent	mostly absent
Inflorescence..	mostly racemiform	mostly corymbiform
Peduncles. . .	1–2.5 cm long, tomentose or scabrid	0.5–5 cm long, glabrous or tomentose
Heads .	medium, 25–30-flowered	small to medium, 12–48-flowered
Involucre...	pubescent or glabrescent	glabrous or tomentose
Outer bracts.	8–12, uniform green	8–18, often paler or white at margin
Inner bracts. .	12–18	10–22
Florets. .	yellow	pink, white, or yellow
Anther appendages	0.5 mm long, oblong	0.8 mm long, lanceolate
Styles.	yellow	purple or yellow
Achenes.	4 mm long, subcompressed or subterete, equally attenuate to both ends	4–5 mm long, subterete, more attenuate upward
Distributional comparison		
	widespread geographically more restricted altitudinally in Switzerland only in the north-west in Italy only on the Austrian frontier in Austria common in N. Balkans widespread	restricted geographically has greater altitudinal range in Switzerland only in the south-east in Italy throughout S. Tirol, but not in Austrian Tirol in Austria only in S. Kärnten in N. Balkans only locally in Krain and Bosnia

Relationship

Crepis incarnata bears such strong general resemblance to *C. praemorsa* that one is at first inclined to follow the precedent set by Fiori (441) of combining the two. But a critical comparison of many specimens reveals the fact that, although the two species overlap in most quantitative characters, yet *C. incarnata* is actually distinct in a number of morphological features (cf. table 15). These may be summarized as follows: *C. incarnata* is characteristically a more slender plant with narrower caudex and smaller leaves which are more often obovate than oblanceolate; the stems, peduncles, and involucre are never scabridulous; the aggregate inflorescence is nearly always corymbiform; the florets are pink or sometimes white (yellow in m.v. 1); the styles are purple (yellow in m.v. 1); the anther appendages are longer and relatively narrower; and the achenes tend to be a little longer, less compressed, and more strongly attenuate toward the apex than toward the base.

Furthermore, the two species differ notably in their ecological relations. *C. praemorsa*, as has been pointed out by Hegi (*loc. cit.*), requires warm but not too sunny exposures and usually occurs at rather low altitudes, whereas *C. incarnata* is often found in open exposures and in subalpine locations, although it is sometimes carried down to very low altitudes where it is then associated with other subalpine "driftlings." In geographic distribution the two species are extremely different, *C. praemorsa* being a widespread east-west migrant, whereas *C. incarnata* is restricted to S. Tirol and closely adjacent areas. The only regions where the two might come in contact are along the Italian-Austrian border and in Kärnten, Krain, and Bosnia. No records, however, are known to me showing that the two species have been collected at the same location, nor are there records of suspected natural hybrids between them. And even if such hybrids were to be reported in the future, it would still remain to be shown that they were capable of producing sufficiently vigorous and fertile offspring to maintain a hybrid swarm in nature.

The question concerning the region of origin of *C. incarnata* is open to debate. It may be assumed that the two species were derived from a common ancestor; but whether the now extinct ancestral species once had a widespread distribution or whether it existed only in Central or S.W. Asia can only be conjectured. Considering the present wide distribution of *C. praemorsa* and the existence in Japan of the closely related *C. gymnopus*, it would seem perhaps more likely that the three species were derived through isolation from a common widespread ancestor.

SECTION 14. MESOPHYLLION

This section consists of 2 perennial and 1 annual species which are characterized by a deeply penetrating root, rather narrow lanceolate or oblanceolate leaves, an erect, slender, or robust stem with short branches near the top and sometimes branched from below the middle or near the base, a compound or simple cymose-corymbiform inflorescence, medium-large to rather small heads, with 5–12 outer involueral bracts which are $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner ones and the inner bracts becoming somewhat thickened and indurate or carinate dorsally, beakless achenes with 10–12 ribs, and white pappus. The 2 perennial species are about equally primitive, but *C. ircutensis* is a taller plant than *C. Bungei* and in the former the stem is branched paniculately, the heads may be a little larger, and the involucre less specialized, although the small number of specimens of *C. ircutensis* make comparisons difficult. For this reason it cannot be stated definitely whether *C. ircutensis* is mat-forming; whereas in *C. Bungei* this is known to be a characteristic feature. This tendency of the roots in *C. Bungei* to form adventitious buds and bear fibers near the crown, and the similarities in leaves and fruits in secs. 14 and 4, certainly indicate a phylogenetic connection between these two sections. *C. tectorum*, a monocarpic species, is obviously close to the two preceding species (cf. figs. 163–165), but it is a more reduced species. This is especially exemplified by its anther tubes, style branches, achenes, pappus setae, and the definitely more specialized inner involueral bracts. These features are associated with an aggressive, weedy habit and a very wide geographic distribution, whereas the two perennials are restricted to the region of origin for the genus and an adjacent area to the east (fig. 162). The karyotypes of *C. tectorum* and *C. Bungei* are closely similar and resemble that of *C. chrysanth* of sec. 4. Hence, this section, with its definitely primitive connections and, at the same time, the advanced aspect of *C. tectorum*, is not only an intermediate group, as its name implies, but is also a bridging group, connecting some of the more primitive and more advanced sections in the genus.

Key to the Species of Section 14

- Plant perennial; root dark brown; involucre 9–12 mm long, the outer bracts lance-linear and the broadest about 1 mm wide at the base; style branches yellow; achenes yellow at the apex; pappus 7–8 mm long.
- Stem branched mostly below or near the middle, the branches mostly long; heads about 30-flowered; outer involueral bracts only 5 or 6.....112. *C. ircutensis*, p. 560
- Stem branched mostly above the middle and often near the top, the branches mostly shorter; heads about 75-flowered; outer involueral bracts about 10. 113. *C. Bungei*, p. 564
- Plant annual; root pale yellowish; involucre 6–9 mm long, the outer bracts linear, very narrow; style branches dark green; achenes not yellow at the apex; pappus 4–5 mm long..... 114. *C. tectorum*, p. 566

112. *Crepis ircutensis* Babc.

Univ. Calif. Publ. Bot. 19: 401, 1941. (Fig. 163.)

Perennial; root slender, woody, dark brown; caudex 3–7 mm long (or longer), 3–5 mm wide (or wider), covered with brown bases of old leaves; stem 2–5 dm high, terete, striate or sulcate, glabrescent, purplish, remotely paniculately branched, lower branches elongated, strict, cymosely 4-branched near the summit, branchlets pedunculate, aggregate inflorescence cymose-corymbiform; caudical leaves 5–7 cm long (or more), about 1 cm wide, oblanceolate, acute, repand-denticulate, shortly petiolate, glabrous, the midvein prominent; lower cauline leaves similar, middle and upper cauline leaves gradually reduced, lance-linear, acute or acuminate, ses-

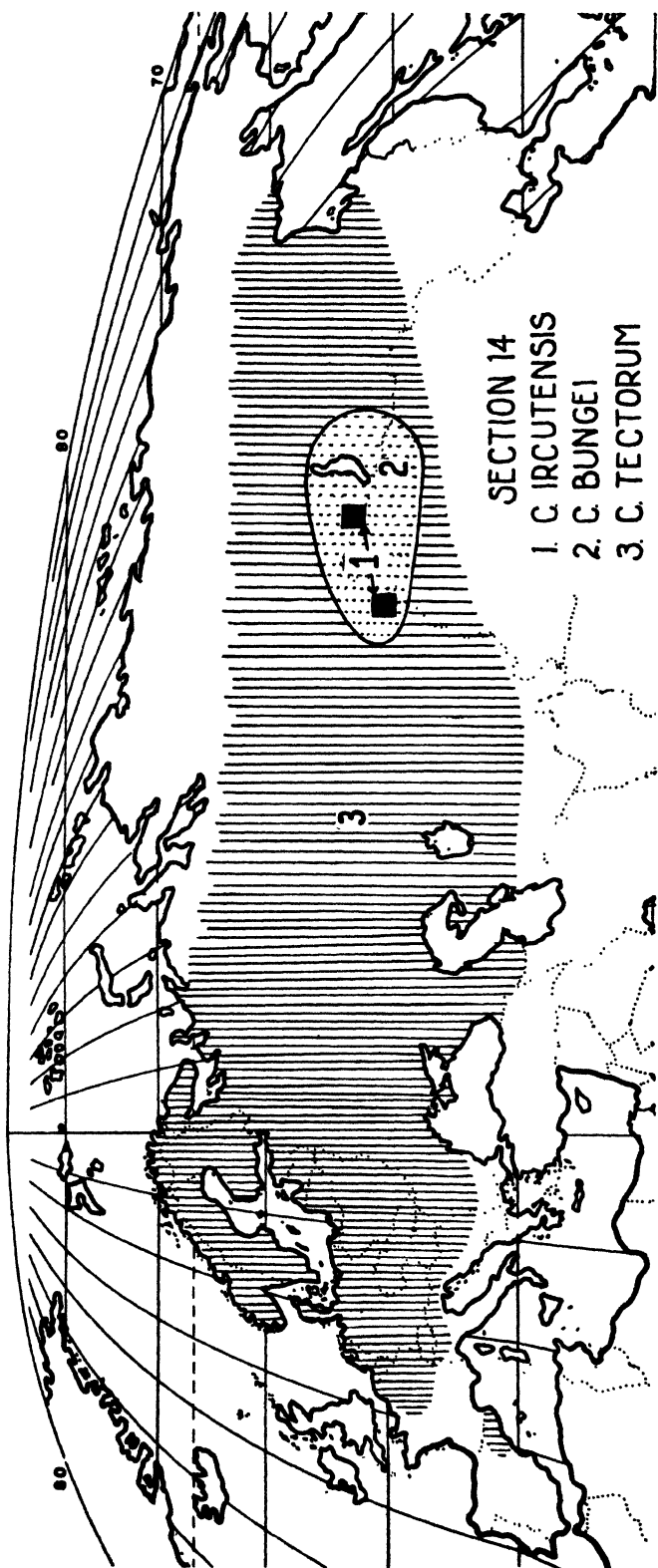


Fig. 162. Geographic distribution of the 3 species in sec. 14. The 2 known stations for *C. ircutensis*, shown by solid squares, lie within the area of *C. bungei* and *C. tectorum*. Based on Goode Base Map No. 201 HC. By permission of the University of Chicago Press.



Fig. 163. *Crepis irtutensis*, from type (B): *a*, upper parts of plant, $\times \frac{1}{2}$; *b*, head in anthesis, $\times 2$; *c*, *c'*, inner involucre bract, outer and inner faces, $\times 4$; *d*, floret lacking ovary, $\times 4$; *e*, anther tube, $\times 8$; *f*, detail of appendages, $\times 32$; *g*, *h*, achene and pappus seta, $\times 8$.

sile, uppermost bractlike; peduncles 4–9 cm long, strict or arcuate, glabrous below, puberulent or gland-pubescent above, with several small bracts near the head; heads erect, medium, about 30-flowered; involucre cylindric-campanulate, 9–12 mm long, 5–6 mm wide at middle in fruit, dark green, canescent tomentulose, gland-pubescent with short black or dark green setules bearing yellow glands; outer bracts 5–6, about $\frac{1}{4}$ as long as the inner, lance-linear, acute; inner bracts 10–14, lanceolate, acute, white-ciliate at tip, glabrous or pubescent and with a fine white median nerve on inner face, becoming slightly thickened and indurate (scarcely spongy-thickened) in fruit; receptacle glabrous; corolla in marginal florets, 13–14 mm long; ligule 2.25 mm wide; teeth 0.3–0.5 mm long; corolla tube 4 mm long, glabrous; anther tube 3.75×1 mm dis.; appendages 0.8 mm long, sagittate, acute; filaments 1 mm longer; style branches about 2 mm long, 0.15 mm wide, yellow; achenes brownish-purple, yellowish at apex, 4.5–5 mm long, 0.8 mm wide, subterete, equally attenuate to both ends, 0.3–0.4 mm wide just below the expanded pappus disk, thinly pale-calloused at the hollow base, about 10–12-ribbed, ribs nearly equal or 2–3 weaker than the others, narrow, rounded, smooth or muriculate near apex; pappus white, about 7 mm long, 2-seriate, setae unequal, coarsest about 40μ , finest about 20μ wide at base, the outer setae finer, rather rigid but pliable, persistent. Flowering Aug.–Sept.; flowers yellow.

S. Siberia (and probably N. Mongolia) in the Sajon Mts.

Monomorphic.

Siberia: Irkutsk Prov., Sajon Mts., along the upper course of the Irkut and Oka rivers, Komarov, Aug. 31, 1902, flowers and fruits (B type, UCf and photo); Altai, Geblcr (NY ex Herb. Hort. Petropol.).

Relationship

Crepis irtutensis may be considered slightly more primitive than *C. Bungei* on account of its taller stature and open, paniculate habit of branching. In involucre and floral characters the two species are closely similar, although the smaller number of florets per head and the much longer, sagittate anther appendages in *C. irtutensis* served to confirm the identification of the two plants from the "Altai" (cited above) which lack mature achenes. *C. irtutensis* is certainly a perennial species. Although the type specimen lacks the root, it is present in the other two specimens seen by me. The root is slender but woody; and, from the appearance of the leaf scars on the caudex, it is evident that one of these plants was in its second year of life when collected, and the other, in its third or fourth. Although the areas of distribution of *C. Bungei* and *C. tectorum* overlap, *C. irtutensis* cannot be considered as a first-generation natural hybrid between them, for the following reasons: (1) The inner involucre bracts of *C. irtutensis* are glabrous on the inner face in the type, whereas they are pubescent in both of the other two species. (2) The heads are about 30-flowered in *C. irtutensis*, but they are 75-flowered in *C. Bungei* and 30–70-flowered in *C. tectorum*. (3) The achenes of *C. irtutensis* are slightly larger than those of *C. Bungei* and much larger than those of *C. tectorum*. (4) The style branches of *C. irtutensis* approach those of *C. Bungei* in size and are very much larger than those of *C. tectorum*. (5) The anther appendages in *C. irtutensis* are nearly twice as long as in *C. Bungei*; they are longer and wider than in *C. tectorum*; and they are different in shape from both the other species. (6) The involucres of *C. irtutensis* resemble those of *C. Bungei* rather than *C. tectorum* in size and in the limited amount of dorsal thickening of the inner bracts. None of the foregoing observations would be expected in an F_1 hybrid between the two species in question; and such a combination of quantitative differences as those mentioned (items 2–5 above) would be very unlikely to occur in a single individual in an F_2 or later

generation, especially if multiple genes were involved in the size differences in question. Therefore, *C. ircutensis* must be considered as a distinct species.

C. ircutensis is a perennial and is similar to *C. Bungei* in leaf shape and in the involucre and achenes. But it is distinct in the relatively small number of florets per head and in the very different anther appendages, as well as in size and habit of the plant. Although the two plants of Gebler from the Altai have the inner bracts pubescent on the inner face, yet this is a variable character in certain other species (cf. *C. nicaeënsis*). Furthermore, *C. ircutensis* occupies the same geographic region as *C. Bungei*, and, since it apparently has similar ecological relations, it probably is isolated from the latter physiologically as a result of the genic differences involved. It is conceivable, however, that *C. tectorum* originated through hybridization between *C. Bungei* and *C. ircutensis*. An investigation of interspecific lethal genes in these three species might throw considerable light on their phyletic relations. Like *C. Bungei*, *C. ircutensis* shows many resemblances to *C. chrysantha* of sec. 4; and this more firmly establishes this section as a bridging group between the more primitive and the more advanced species of the genus.

113. *Crepis Bungei* Ledeb.

Ex DC., Prod. 7: 164. 1838. (Pl. 12; fig. 164.)

Perennial, mat-forming by spreading from root sprouts; caudex 5–10 mm long, 4–8 mm wide, simple or 1-furcate, prolonged into a slender vertical or oblique tap-root bearing fibers which sometimes generate adventitious buds; caudical leaves up to 10 cm long, 1.5 cm wide, oblanceolate, acute or obtuse-mucronate, dentate or denticulate, teeth often retrorse, attenuate in a short narrowly winged petiole, like stem canescent-tomentulose or glabrescent; cauline leaves similar or sessile, uppermost entire, acuminate, bractlike; stem 1–4 dm high, erect, terete, striate, fistulose, few-branched above the middle, the branches short, usually forming a few-headed congested cyme; peduncles 0.7–6(10) cm long, bracteate, \pm thickened, sulcate, tomentulose and gland-pubescent near head; heads erect, rather large, about 75-flowered; involucre 9–12 mm high, 4–5 mm wide near base in anthesis, campanulate; outer bracts 10, unequal, longest nearly $\frac{1}{2}$ as long as inner bracts, remote, often merging with the bracts of the peduncle, lance-linear, acute or acuminate, scarious-margined, \pm tomentulose and gland-pubescent; inner bracts 12–16, lanceolate, obtuse and ciliate at tip, in 2 or 3 ranks, all or innermost broadly scarious-margined, dorsally densely gland-pubescent, hairs pale or dark, glands yellow, becoming obscurely \pm carinate and sometimes slightly spongy-thickened dorsally but not conspicuously changed, ultimately reflexed, ventrally pubescent with short appressed hairs or glabrescent; receptacle areolate, glabrous or with occasional very fine caducous cilia; corolla 14–17.5 mm long; ligule 2–2.75 mm wide; teeth 0.2–0.4 mm long; corolla tube 4–6 mm long, glabrous or sometimes with a few very short (less than 0.1 mm) acicular hairs; anther tube yellow, (4)5 \times 1.25 mm dis.; appendages 0.6–1.0 mm long, oblong or oblong-lanceolate; filaments 1–1.5 mm longer; style branches 2.5–3.5 mm long, 0.15 mm wide, yellow; achenes reddish or purplish-brown, yellow at summit and base, 4–5 mm long, 0.75 mm wide, fusiform, moderately attenuate to both ends, with slightly expanded pappus disk and calloused hollow base, subterete or obscurely angular, 10–12-ribbed, ribs rather prominent, rounded, finely rugulose under lens; pappus white, 7–8 mm long, copious, rather firm but pliable, 2-seriate, setae unequal in width, persistent. Flowering June–July; flowers yellow. Chromosomes, $2n = 8$.

Hieracium strictum Ledeb., Fl. Alt. 4: 132. 1833 non *C. stricta* Scop.
Crepis Bungeana C. A. Mey., ex DC., Prod. 7: 164. 1838.

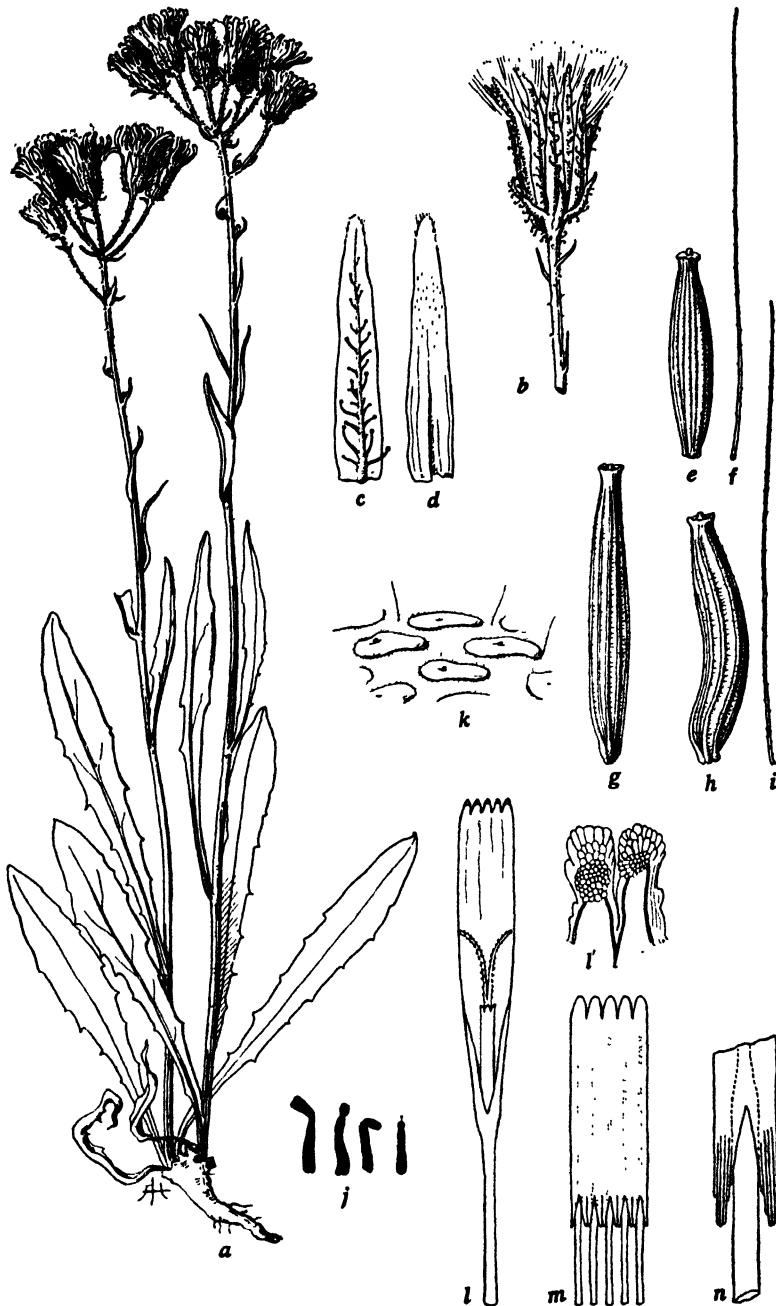


Fig. 164. *Crepis Bungei*, a, l-n, from Karo 369 (Mo 119574); b-f, from authentic spec. in herb. DC. Prod. "ad fluv. Tineum," Turczaninow in 1835 (cf. pl. 12); g-k, from hort. genet. Calif. 1827 (UC 494359): a, plant, $\times \frac{1}{2}$; b, mature head, $\times 2$; c, d, inner involucre bract, outer and inner faces, $\times 4$; e, f, immature achene and a pappus seta, $\times 8$; g-i, 2 mature achenes and a pappus seta, $\times 8$; j, somatic chromosomes, $n = 4$, $\times 1250$; k, detail of receptacle, $\times 25$; l, floret lacking ovary, $\times 4$; m, detail of ligule teeth, $\times 25$; n, detail of appendages, $\times 32$. Cf. pl. 12, which shows authentic specimens in herb. DC.

C. salicifolia Froel., ex DC. (*loc. cit.*, 169).

H. uliginosum Turcz., Fl. Baikal.-Dahur. 2: 161. 1856.

Berinia stricta Sch. Bip., Pollichia 22-24: 317. 1866.

Hieraciodes strictum O. Kuntze, Gen. 1: 345. 1891.

S. Siberia from the Altai reg. to Transbaikalia and in N. Outer Mongolia; in swamps and moist meadows and on riverbanks.

Monomorphic.

Siberia: Altai reg., *Bunge misit 1887* (DC) type; Altai, Koseh-Agacz, subsaline meadow, Krylov in 1903 (G); Altai, Oirot reg., *Schischkin* in 1936 (G); Baikal reg., swamp, *Turczaninow* in 1830 (DC); near Lake Baikal, *Turczaninow* in 1835 (DC); along Tineun R., *Turczaninow* in 1835 (DC), as *H. umbellatum*; Transbaikalia, mouth of Kiachta R., wet marsh, *Turczaninow* in 1823 (DC); Transbaikalia, near Kiachta, *Turczaninow* in 1835 (Mu, PC); Transbaikalia, Nercysynsk, moist meadows along Nersey R., *Karo 369* (B, VG, Mo). **Outer Mongolia:** Chan-gai (Khan-gai) Mts., steppe valley of the Halzyngin-Bulyk R. near Zanch-gogen, *Pavlov 1860* (Mose); Outer Mongolia, meadows along the Ohron R., in moist places, *Pavlov 1500* (Mose); Mongolia, gravelly places near the Murin-gol R., *Pavlov 1024* (Mose); N.W. Mongolia, 47° N., 104-105° E., dry meadow near the Dshargalante R., *Krashenninnikov* in 1925 (NY); *ibid.*, seeds, plants grown in hort. genet. Calif. 26.1827-47, 2n = 12 (UC); N. Mongolia, Urga, vicinity of Ulan-Bator-Huto, right bank of the Tolah R., opposite Santgei (?), meadow near willows, *Ikonnikov-Galitzky 340* (UC); N. Mongolia and Hangai, banks of the Haitu-Tamir and Lagan-Kura rivers, among *Iris ensata*, *Ikonnikov-Galitzky 319* (UC).

Relationship

Crepis Bungei has a fairly primitive involucre, although there is a definite tendency for the inner involucreal bracts to become dorsally spongy-thickened and carinate. It is sufficiently close genetically to a tetraploid species of the same geographic region, *C. crocea*, to justify the hypothesis that *C. Bungei* is one of its parents. With *C. Bungei* it has been hybridized artificially and the F₁ hybrids are vigorous but exhibit a very low degree of fertility. The probability that *C. Bungei* and *C. oreades* are the parents of *C. crocea* is discussed under the latter species (p. 507).

There is a general similarity in chromosome morphology between *C. Bungei* and *C. tectorum*, and it has been suggested by Navashin and others that the two may be closely related. The evidence from comparative morphology certainly supports this view; but the further suggestion that *C. Bungei* may have been derived from *C. tectorum* is not in agreement with the evidence on phylogeny. *C. Bungei* is undoubtedly a much older species, of more limited distribution, whereas *C. tectorum* has become a widespread species through the advantage of the annual habit, and along with this has gone further reduction and specialization. This concept of the relative ages of *C. Bungei* and *C. tectorum* is strengthened by the discovery of the other more primitive species, *C. ircutensis* (q.v.).

114. *Crepis tectorum* L.

Sp. Pl. 2: 807. 1753, non Vill., nec Huds. (Fig. 165.)

Annual, sometimes persisting over winter, 0.3-9.7 dm high with slender tapering root; basal leaves rosulate, numerous or few, ± ephemeral, up to 15 + cm long, 4 + cm wide, lanceolate or oblanceolate, acute, denticulate, dentate or runcinate-pinnatifid or lyrate-pinnately or bipinnately parted with remote unequal lanceolate or linear acute lobes, tapering into a winged petiole, glabrous, gabraescent, ± tomentulose or ± puberulent on both sides with short fine glandular or glandless hairs; lower cauline leaves similar, middle cauline leaves lanceolate or linear, acute, sessile, usually acutely auriculate, uppermost linear with revolute margins or bract-like; stem erect, fistulose, sulcate or striate, ± tomentulose, sometimes shortly and

finely pubescent, paniculately or corymbosely branched above the middle or from the very base, or central axis short with numerous strictly erect branches from near base, the branches many-headed or rarely pedunculate, or branches diffuse, arcuate or semiprocumbent, few- or many-headed; peduncles 0.3–7 cm long or up to 17 cm in rare pedunculate-branched forms, slender or very slender, slightly enlarged at base of head, tomentulose or tomentose, sometimes hispidulous; heads erect, medium or small, numerous or few, 30–70-flowered; involucre cylindric-campanulate, up to 9 mm long and 7 mm wide at middle in fruiting heads; outer bracts about 12, unequal, longest $\frac{1}{3}$ as long as inner ones, sometimes with several subtending ones, subulate, like inner ones \pm tomentose and hispidulous, often becoming scarious and lax; inner bracts 12–15, lanceolate, acuminate, in 2 series, inner ones broadly membranous-margined, white ciliate at tip, becoming dorsally keeled and spongy-thickened near base, ventrally \pm pubescent, ultimately reflexed; receptacle areolate, subfimbriate, fimbriae shortly and very finely ciliate; corolla up to 13 mm long; ligule up to 2.5 mm wide; ligule teeth 0.2–1 mm long; corolla tube 3–3.75 mm long, pubescent with short (up to 0.2 or 0.3 mm long) stalked acicular hairs; anther tube (2.3)3 \times 0.8(1) mm dis.; appendages 0.5–0.6 mm long, oblong, obtuse; filaments 0.4–0.7 longer; style branches 0.9–1.5 mm long, 0.1 mm wide, dark green, yellow on inner face; achenes (2.5)3–4(4.5) mm long, dark purplish-brown, fusiform, terete, rather strongly attenuate below the pale expanded pappus disk but scarcely short-beaked, constricted at the narrow hollow pale-calloused base, 10-ribbed, ribs rounded, finely spiculate, especially near summit; pappus 4–5 mm long, white, 1-seriate, fine, soft, early deciduous or semipersistent. Flowering May–Aug.; flowers yellow without red on ligules. Chromosomes, $2n = 8$.

Crepis murorum S. G., Gmel., Iter Ros. 1: 138. 1774.

C. Dioscoridis Pollich, Palat. 2: 399. 1777, non L.

C. varia Moench, Meth., 534. 1794.

C. Lachenalii Gochn., Tent. Cichor. 19. t. 3. 1808, non Gmel.

C. integrifolia Vest., Flora 3: 7. 1820; Gaud. ex Colla, Herb. Pedem. 3: 500. 1834 in obs.

C. angustifolia Urv., Enum. Pl. Arch. 101. 1822.

Hieracium tectorum Karsch, Fl. Westf. 331. 1853.

Hieraciodes tectorum O. Kuntze, Gen. 1: 346. 1891.

C. barchhausioides Rouy, Fl. Fr. 9: 227. 1905 ex descr.

Most of Europe from 70° N. lat., southward into E. Spain, middle France, N. Italy, the middle Balkan Pen., and S. Russia to the Caucasus; the greater part of Siberia from the Urals, N. Kazakhstan, and Turkestan eastward to Manchuria and Kamchatka. Introduced into the latter region, according to both Hulten and Komarov, it is uncertain just how far east of the Baikal region the species is indigenous. It has become naturalized in other continents, notably in North America and Australia.

This widespread and often abundant species of the lowlands occurs under such great diversity of conditions that ecological forms are of frequent occurrence. It grows on soils deficient in lime as well as on calcareous soils. Among the rich collections of the University of Moscow the following diverse habitats are represented: among standing grain, fallow fields, wastelands, forest clearings, wooded slopes, moist forest, sandy places, dry stream bed, moist meadow, limy clay soil, lakeshore, seashore, sandbanks in flooded meadow, old walls and roofs, etc. Furthermore, the plant is not infrequent in mountainous regions where still other ecological forms are produced. No effort has been made to list the ecads of this polymorphic species, except for some types which have previously received Latin names as varieties or forms. Some of the numbered variants listed below are of this nature (cf. m.v. 1–4), whereas others are certainly or very probably ecotypes (cf. m.v. 6–8). None of the

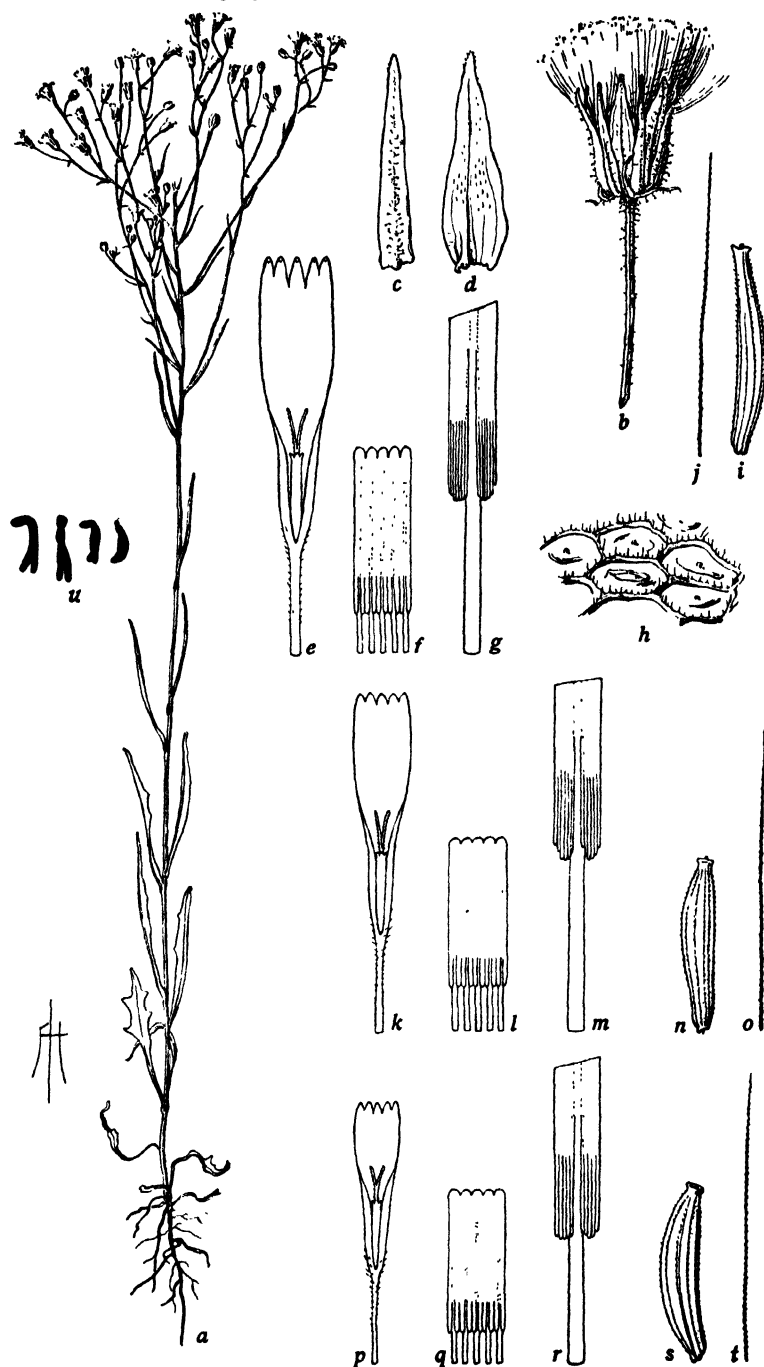


Fig. 165. *Crepis tectorum*, a-j, from Sireischikov 5078 (Mosc); k-o, from Baehrendts in 1900 (Minn 217933); p-t, from Th. Fries in 1925 (UC 296060); u, from hort. genet. Calif. 1498 (grown from seed received from Copenhagen Bot. Gard.): a, plant, $\times \frac{1}{6}$; b, head, $\times 2$; c, d, inner involucre bracts, outer and inner faces, $\times 4$; e, floret lacking ovary, $\times 4$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, detail of receptacle, $\times 25$; i, j, achene and pappus seta, $\times 8$; k, l, m, n, o, p, q, r, s, t, achene and pappus seta, $\times 8$; u, somatic chromosomes, $n = 4$, $\times 1250$.

latter, however, is sufficiently distinct morphologically to warrant its recognition as a subspecies.

Scandinavia: N. Norway, Finmarkia, Alten (= Alten Kirke), 70° N., *Fridtz* in 1884 (Minn) m.v. 1, 2; *ibid.*, Høngen Bardo (Bardo is about 69° N.), *Landmark* in 1899 (UC) m.v. 1, 2; W. Norway, Søndfjord, *Landmark* in 1902 (Minn) m.v. 1; S.E. Norway, Oltsfold, Fem Sjø, *Th. Fries* (K) m.v. 1, 2; S. Sweden, Upsala, waste and cultivated land, *Ahlberg* in 1865 (K) m.v. 2; *ibid.* (†), *Linné 10* (L) type = m.v. 1; S.E. Sweden, Vargön, Venersborg, near Göteborg, *Tidestrom* in 1894 (UC); S. Sweden, near Stockholm, in 1843 (K); *ibid.*, Örebro, *Bagenholm* in 1897 (Minn) m.v. 3; *ibid.*, Örebro, Latorp, *Bagenholm* in 1895 (Minn); Oland I., Thorshurda, *Areskog* in 1888 (Minn) m.v. 6; *ibid.*, Köping, *Holmerts* in 1918 (UC) m.v. 6; Gotland I., Follingbo, *Fries* in 1925 (UC) m.v. 7. **France:** Seine et Oise, Jouy en Josas, wall, *Rouy* in 1874 (K); Fontainebleau, walls, *Gay* in 1833 (K) m.v. 1; Versailles, *Bue* in 1849 (DS); Strasbourg (DS). **Germany:** Hamburg, Wandsbek, *Kausch* in 1879 (UC) m.v. 1; Prussia, Breslau, *Krause* in 1878 (UC); S. Prussia, *Stapf* in 1885 (UWG) m.v. 3; Saxony, Dresden, walls, *Reichenbach* in 1831 (K); Palatinate, near Deidesheim, *Schults Bip.* in 1849 (Bur). **Switzerland:** Valle St. Nicolai, *Schleicher* (Oxford, Druce) m.v. 2; Valais, between Italden and St. Nicholas, *Morthier* in 1878 (Bur); Basse-Engadine, Lavin, 1430 m, *Favrat* in 1867 (Bur); Valais, Simplon, at base, *Wolf* in 1876 (Bur). **Italy:** Trentino, Brixen, near station, *Moggridge* in 1870 (K) m.v. 2; S(†) Italy, among rocks around "Argentinum," *Nestler misit*, 1826 (DS). **Greece** (†): Archipelago, *d'Urville 74b* in 1821 (DC). **Austria:** Rossatz, *Krebs* in 1897 (Minn); Tirol, Val di Sole, *Burnat* in 1873 (Bur); Tirol, Lienz, field, *Ganders* in 1869 (K) m.v. 2. **Serbia:** Belgrade, environs of Pancic, Kilabvo, sand, *Servio* in 1875 (Bur). **Bulgaria:** near Philippope, Bunardjik hill, *St. Georgieff* in 1892 (Sofia); Varna dist., near Gebedje, *Jordanoff* in 1926 (Sofia); Sumen dist., Kabijuk, *Jordanoff* (Sofia); Varna dist., Sinbei, *Davidov* in 1906 (Sofia-M); Deli Orman, between Gebedje and Emirler, hills, *Davidov* in 1906 (Sofia-M); E. Balcan, Mt. Avrenska planina, *Davidov* in 1904 (Sofia-M). **Czechoslovakia:** Trencsen, Iktebrucker Balinhof, *Brancsik* in 1902 (Po); Brünn, *Schur 9038* (K) m.v. 1; Transylvania, Döbling, *Schur 2354* (K) m.v. 2. **Poland:** Lithuania, Nowogrodek dist., Wojnow, *Dybowski* in 1894 (K) m.v. 2. **Finland:** Kantvik, Nylandia, dry field, *Lindberg 1000* (K, UC) m.v. 1. **Russia:** E. Lapland, Ponoï, 67° N., *Fellman 142* (K) m.v. 8; *ibid.*, near Keret, 66° N., sandy place on marine island, *Fellman 143* (K) m.v. 8; Archangel Prov., Ssolowetsk I., Kola Pen., *Pohle* in 1911 (B) m.v. 8; Vologda Prov., *Ivanitzki* in 1880 (Mosc); Tver Prov., Tver dist., *Popov 578* (Mosc) m.v. 2, 3, p.p.; Jarosslawl Prov., Jarosslawl, *Petrovski 368* (Mosc) m.v. 2; Smolensk Prov., fields, fence rows, walls, *Tichomirov 437* (Mosc); Smolensk Prov., Viasem dist., edge of birch forest near Klucheevo, *Pletner 211* (Mosc); Smolensk Prov., near Mrudzanov, *Zinger 1294* (Mosc) m.v. 2; Moscow Prov., Kin dist., shore of Senega Lake, *Sireischikov 5078* (Mosc); Vladimir Prov., Aleksei dist., *Fleurov 502* (Mosc) m.v. 2; Tambov Prov., moist forest, *Dmitriev 324* (Mosc); Tula Prov., common, *Zinger and Koshevnikov 429* (Mosc); Riazon Prov., Devnovo, *Meshaiev 409* (Mosc) m.v. 10; Penza Prov., watershed of Moksha R., *Kosmovski 407* (Mosc); Orel Prov., Orel Co., between Senkovsk and Tagin, bank of Oka R., *Kosmovski 318* (Mosc) m.v. 3; Niszhnegovod Prov., Balachn dist., *Zinger 1306* (Mosc) m.v. 2; Kostroma Prov., Galitch Co., near Isakovo, *Sahadovski 873* (Mosc) m.v. 4; Simbirsk Prov., Simbirsk Co., dry stream bed, *Zinger 1307* (Mosc); Catherinoslav Prov., near Alexandrowski, along Konkam R., *Gruner* (Mosc) m.v. 9; Turgai Prov., Turgalo R., sandbanks in flooded meadow, *Krinkov* in 1898 (Mosc) m.v. 2; W. Ukraine, near Kiev, field, *Gowe* in 1890 (UC); Saratov Prov., Kamishinsk Co., near Lopuchovka, wooded slopes, *Zinger 1303* (Mosc) m.v. 1. **Dzungaria:** *Schrenk* (K) m.v. 3. **Siberia:** Tomsk Prov., Marein Co., near Tiuchtet, dry meadows among birch trees, *Kutschеровskaja 58* (UC); Altai reg. *Ledebour* (K); *ibid.*, *Duhmberg 336* (B); Irkutsk, in 1876 (K) m.v. 1; Irkutsk, Niszhni dist., near Gromov, field borders, *Kristofovits* in 1910 (UC); Transbaikalia, *Stevens* (K); Kamchatka, watershed of Kamchatka R., forest, *Komarov and Besais 4472* (K) m.v. 2; Kamchatka Pen., *Komarov 2785* (B). **Manchuria:** Amur R., around Sakhalin, *Karo 1653* (K) m.v. 3; no def. loc., *Bohnhof* in 1898–1899 (K, B). **British Columbia:** Fraser R., between Soda Creek and Quessel, *McCabe* in 1934 (UC). **Alberta:** Stettler dist., Bashaw, *Brinkman 2354* (US). **North Dakota:** Dickinson, *Holgate* in 1908 (G); Bottineau Co., Willow City, *Lunell* in 1914 (US, Minn). **Michigan:** Lansing, *Bailey* in 1882 (G); Detroit R., Isle aux Peches, *Wheeler* in 1892 (US, G).

Minor Variants of *C. tectorum*

1. (*C. tectorum* var. *vulgaris et valida* E. Mey., ex Bisch., Beit. 273. 1851; *C. tectorum* var. *typica* Beck-Mann., Fl. Nied. Oest. 2: 1271. 1893 et var. *genuina* Fiori, Fl. Anal. Ital. 3[2]: 435. 1904.) These all correspond in habit to the type of the species in Herb. Linn. Upper radical and lower cauline leaves lanceolate, runcinate; middle cauline leaves sinuate-dentate; uppermost leaves linear, entire, often acutely auriculate; stem paniculately branched above, many-headed. *Linné 10* (L) S. (†) Sweden; ex Herb. Petropol. (K) Irkutsk, Siberia; *Schur 9038* (K) Brünn, Czecho-

slovakia; *Tratchkov and Poganka 820* (Mosc), fields, roadsides, roofs, Orel Prov., central Russia; *Lindberg 1000* (K, UC) dry field, Nylandia, Kantwik, Finland.

2. (*C. tectorum* var. *segetalis* Roth, Tent. Fl. Germ. 2[2]: 254. 1793; *C. tectorum* var. *stricta* Schultz, Fl. Starg. Suppl. 41. 1819, non Scop.) Somewhat reduced forms of the above often due to crowding. Lower leaves lanceolate, dentate; upper leaves linear, not auriculate; stem paniculately or corymbosely few-branched above, few-headed. *Komarov 4472* (K) forest reg., watershed of Kamchatka R., Kamchatka, Siberia; *Krinkov* in 1898 (Mosc) sands along Turgalo R., Turgai Prov., Russia; *Gander* in 1869 (K) field, Lienz, Tirolia; *Schur 2354* (K) Döbling, Transylvania.

3. (*C. tectorum* var. *gracilis* Wallr., Sched. Crit. 430. 1822; *C. Lachenalii* Gochn., loc. cit. non Gmel.) More extremely reduced forms of the above. Leaves mostly linear, entire; stem very slender, 1-4(6)-headed. *Schrenk* (K) Dzungaria, W. Mongolia; *Kosmovski 818* (Mosc), along Oka R., Orel Prov., central Russia; *Bagenholm* in 1897 (Minn) Orebro, S. Sweden.

4. (*C. tectorum* var. *clata* Ledeb., Fl. Ros. 2: 823. 1844-1846.) Very robust plants: "larger in all parts; cauline leaves lanceolate, sagittate with rather long auricles; panicle corymbosely many-branched." *Chistiakov* in 1862-1865 (Mosc) Catherinoslav Prov., S. Russia; *Szchadovski 873* (Mosc) field, Kostroma Prov., central Russia.

5. (*C. integrifolia* Vest, loc. cit.; *C. integrifolia* Gaud., loc. cit.; *C. barckhausioides* Rouy, loc. cit.) A form with somewhat longer, more attenuate achenes than in most forms. Basal leaves short, lanceolate, petiolate; cauline leaves linear; stem simple, few-headed. Two specimens, apparently this species, were seen in Herb. Orto Bot. Naples; one may be the type of Vest, the other is labeled *C. integrifolia* Gaudin; data on localities are lacking, but Vest's description states that his type was a garden plant, the country of origin being unknown.

6. (*C. tectorum* fa. *pygmaea* Sjöstr., ined. ♀) Plant 3-8 cm high, divaricately branched from base, branches short, leafy; lower leaves lanceolate, pinnatifid or bipinnatifid, dentate or denticulate; upper leaves linear; leaves, stems, and involucre finely gland-pubescent; heads and involucre typical of the species; corolla 11 mm long; ligule 1.75 mm wide, teeth 0.25-0.4 mm long; corolla tube 3 mm long, pubescent with short acicular hairs; anther tube 2.4-0.9 mm dis.; appendages 0.5 mm long, oblong, obtuse; filaments 0.6 mm longer; style branches 1.25 mm long, 0.1 mm wide, dark green, yellow on inner face; receptacle glabrous (♀); achenes 4 mm long; pappus 4-5 mm long. A distinct genetic type or ecotype, known only from Oland I., Sweden. *Areskog* in 1888 (Minn) Thorshurda; *Bagenholm* in 1894 (Minn) Thorshurda; *Baehrendts* in 1900 (Minn, Po) Kastlosa, allvaret; *Holmertz* in 1918 (UC) Köping; *Ahlberg* in 1924 (UC) Vichelby, Oland I., Sweden.

7. (*C. tectorum* var. *glabrescens* Neuman, ined. ♀) Another island ecotype which maintains its characteristic features in garden cultures, but apparently it is a misnomer, as the plants seen by me, although not including the type, are pubescent throughout. Plants 0.8-2 dm high; leaves narrowly lanceolate to linear, denticulate or entire, like stems and involucre finely pubescent with short fine glandular or glandless hairs; stems 1, few-headed with few basal leaves, or several from a leafy rosette, paniculately branched, branches slender, few-headed; heads small; involucre 7-8 mm high; receptacle shortly and finely ciliate; corolla 8.5 mm long; ligule 1.5 mm wide, teeth 0.2-0.45 mm long; corolla tube 3 mm long, pubescent with short acicular hairs; anther tube 2.3 x 0.9 mm dis.; appendages 0.5 mm long, oblong, obtuse; filaments 0.4-0.5 mm longer; style branches 0.9 mm long, 0.1 mm wide, dark green, yellow on inner face; achenes 2.75 mm long; pappus 4-5 mm long. *Fries* in 1925 (UC) Follingbo, Gotland I., Sweden; ex hort. genet. Calif. 28.1702-3 (UC).

8. (*C. tectorum* var. *nigricans* Ruprecht, Diatr. Petrop. [Symbol. 147] ex Rupr., in litt.) Apparently another ecotype of reduced stature. Plant 0.8 dm high, simple-stemmed, 4-headed, peduncles very short; basal and cauline leaves lyrate-pinnatifid except uppermost 3 or 4, which are linear, entire, glabrescent; involucre 7-8 mm high; florets 11-12 mm long; style branches green. *Fellman 143* (K) sandy place on marine island near Keret, 66° N., E. Lapponia. On same sheet with the last is another plant, *Fellman 142*, which is very similar except leaves finely denticulate to entire; collected at Ponoj, about 67° N., E. Lapponia, Russia.

9. Heads very small and involucre notably canescent-tomentose; plant 5 dm high, the simple stem very shortly corymbosely branched near summit; lower leaves lacking, middle cauline leaves shortly petioled, lyrate-pinnatifid with linear acuminate terminal lobe and remote acute lateral lobes, tomentulose and puberulent; upper cauline leaves filiform; peduncles short, very slender; involucre 7 mm high, 4 mm wide in mature heads, finely hispidulous; heads about 50-flowered; corolla 9 mm long; style branches green; achenes 2.5-3 mm long, slender, rather strongly attenuate upward; pappus 4.5 mm long, very fine. *Gruner* (Mosc) near Grigorjewka, on Konkam R., Alexandrowski dist., Catherinoslav Prov., S. Russia.

10. Resembles *Crepis Dioscoridis tubaeformis* in its most extreme form; central axis short, branched from near base, the branches long, fastigiate, 1-3-headed, with few or no leaves; lower cauline leaves linear, acuminate, denticulate or entire, glabrous or glabrescent; stem and branches

glabrescent; peduncles tomentulose near heads; heads few, medium, about 60-flowered; florets 11 mm long; ligule teeth 1–2 mm long; style branches green; achenes lacking. Probably an abnormal genetic type. *Meshaiev 409* (Mosc) Devnovo, Riazan Prov., central Russia.

Relationship

Crepis tectorum has as its closest relatives *C. ircutensis* and *C. Bungei*, and these three comprise a natural connecting group between more primitive species, such as *C. chrysantha*, and the more advanced species of the genus. *C. tectorum* is an aggressive, weedy, monocarpic plant, exhibiting certain resemblances to strictly annual species, such as *C. capillaris*. But it differs strikingly from *C. capillaris* in an important adaptation, viz., seed longevity. Whereas the seeds of *C. capillaris* remain viable for several years, those of *C. tectorum* lose the ability to germinate within a year or two after maturation. In *C. capillaris* the seeds normally germinate in the spring after 250 to 270 days of dormancy. But in *C. tectorum* they germinate soon after maturation, and the rosettes live over the winter, the plants flowering the following spring or summer. In this and certain other features *C. tectorum* shows resemblance to *C. nicaeensis*, *C. biennis*, and *C. ciliata*, as well as to *C. Bungei*. But with none of these other species is the resemblance in chromosomes as strong as with *C. Bungei*; and both *C. Bungei* and *C. ircutensis* are most like *C. tectorum* in ensemble.

The discovery by Hollingshead (Genetics 15: 114–140, 1930), through crosses between *C. capillaris* and *C. tectorum*, of an interspecific lethal gene in the latter species suggests the possibility that this or a similar gene may have been an important factor in isolating *C. tectorum* from *C. Bungei* and *C. ircutensis* during the period of their differentiation. The experimental investigation of this question would be a very worth-while project.

SECTION 15. PSILOCHAENIA

The 10 North American species in this section comprise a more heterogeneous assemblage than any other section of the genus. But they have certain common attributes which warrant their inclusion in the same section. They all have the same basic chromosome number, $x = 11$, a number not found in any other section; and they are all believed to have had their origin through interspecific hybridization between Asiatic species with lower chromosome numbers, $n = 7$ and 4 or $n = 5$ and 6. Several different Asiatic species exhibit sufficient resemblance to one or another of these American species to suggest that they, or species closely similar to them, were the parents of the original hybrids in which doubling of the chromosome number occurred to produce $2n = 22$. The fact that these putative original parents are quite diverse, representing 6 different sections, is sufficient in itself to explain the heterogeneity of this group. These species fall naturally into 4 subgroups: (1) *C. monticola*, *C. occidentalis*, *C. Bakeri*, and *C. modocensis*; (2) *C. pleurocarpa*, *C. acuminata*, and *C. atribarba*; (3) *C. intermedia* and *C. barbiger*; (4) *C. runcinata*. The 9 species in subgroups 1–3 have the common characteristics of being very deep-rooted (cf. *C. occidentalis*, fig. 167, a). Immediately after germination of a seed the radical penetrates downward very rapidly to a depth of 1 to 2 dm. The deep subterranean root system of mature plants was found to be a real obstacle to their successful transplantation from the wild to the genetics garden. All 9 species occur in regions deficient in summer rainfall and mostly on mountain sides or dry plains. *C. runcinata*, on the other hand, occurs in a region of some summer rainfall in the eastern part of its range and in the Rocky Mts., and in the Great Basin region it is often found in swampy meadows and in alkali bogs. The root is usually shorter and more fleshy in this species and little difficulty was encountered in transplanting from the wild. Each of the 7 species in subgroups (1) and (2) has a 22-chromosome "diploid" form, and associated with it are numerous polyploid forms which are often apomictic. The 2 species in subgroup (3) are composed entirely of polyploid forms which have been derived from hybridization between 2 or more of the first 7 species. On the other hand, *C. runcinata* apparently exhibits no polyploidy whatever, even though it is highly polymorphic. In all the specimens thus far examined the chromosome number was $2n = 22$. Evidently the history of *C. runcinata* has been very different from that of the other 9 species.

(1) The 4 species comprising this subgroup are more primitive than those of subgroup (2) on the basis of size of heads, type of involucre, length of outer involucre bracts, and size of florets and fruits. *C. monticola* shows some resemblance to *C. kashmirica* (sec. 2), especially in the hairy involucre and the columnar, strongly ribbed achenes. *C. occidentalis* is reminiscent of *C. oreades* (sec. 11) in habit of the plant, in the 22-chromosome form at least, also in type of involucre and especially in the dense gray tomentum on leaves and involucres. *C. Bakeri* shows some resemblance to *C. Bungei* (sec. 14) in inflorescence and pubescence of the involucre; but it is probable that the actual parental species are extinct. *C. modocensis* is reminiscent of *C. hokkaidoensis* (sec. 4) in its achenes and involucres.

(2) The 3 species in this subgroup have much narrower involucres than the species in (1) and have fewer inner bracts and fewer florets in a head, at least in the 22-chromosome forms. *C. pleurocarpa* does not resemble any known Asiatic species sufficiently to warrant its consideration as a parent; and the restriction of the 22-chromosome form of *C. pleurocarpa* to serpentine and similar formations in the Klamath region suggests that it may be an older species than the other two members of this subgroup. *C. acuminata* and *C. atribarba* show sufficient resemblance to

C. flexuosa (sec. 12) to suggest that this species may have been one parent of the two original 11-chromosome hybrids that gave rise to new species through chromosome doubling. In *C. atribarba* there is also some resemblance to *Youngia tenuifolia* (Willd.) (see Part I, p. 158).

(3) The 2 species in this subgroup are agamospecies, each comprising a series of polyploid apomictic forms. The species probably involved in the ancestry of these hybrid polyploid forms are discussed under *C. intermedia* and *C. barbiger*.

(4) *C. runcinata* is sufficiently similar to *C. gymnopus* and *C. praemorsa* (sec. 13) to indicate that the three species may have had a common ancestor. The ecological relations of *C. praemorsa* are very similar to those of *C. runcinata*.

The descriptions of the species in this section are condensed from the monograph on the American species (B. and S., 504), in which the distribution of the species is extensively treated and fully illustrated.

Key to the Species of Section 15

- A Stem and leaves glabrous or glaucous or sometimes hispidulous; cauline leaves generally all reduced, narrow, inconspicuous, or rarely the lowest one similar to the caudical leaves; mature involucre turbinate-campanulate.....124. *C. runcinata*, p. 604
- AA Stem and leaves at least slightly tomentose with a fine appressed tomentum, and often hirsute, setose, or gland-pubescent as well; cauline leaves at least 1-3, usually well developed (except in *C. pleurocarpa*); mature involucre narrowly or broadly cylindric.
 - B Herbage and involucre slightly tomentulose and shaggy-hirsute with long (1-3 mm) gland hairs; inner involucral bracts long attenuate, their tips not folded over the florets in the buds; outer bracts lance-linear.....115. *C. monticola*, p. 574
 - BB Herbage and involucre sometimes setose or gland-pubescent, but the hairs, if glandular, short; inner bracts somewhat attenuate toward the apex, acute or acuminate, folded over the florets in the buds; outer bracts mostly lanceolate or ovate-lanceolate.
 - C Involucral bracts densely beset with blackish, whitish, or yellowish, curved or crisp glandless setae, or, if with few or no setae on the involucre, the basal part of the stem and the petioles conspicuously setose; achenes weakly ribbed or merely striate.
 - D Stems 0.6-3.5 dm high; inflorescence of 1-9 heads; involucre with 8-15 inner bracts and 10-60 florets; longest outer bracts $\frac{2}{3}$ - $\frac{3}{4}$ as long as the inner bracts.....118. *C. modocensis*, p. 584
 - DD Stems 2.5-6 dm high; inflorescence of 6-70 heads; involucre with 5-10 inner bracts and 6-20 florets; longest outer bracts $\frac{1}{4}$ - $\frac{2}{3}$ as long as the inner bracts.....123. *C. barbiger*, p. 602
 - CC Involucral bracts glabrous, tomentose, gland-pubescent, or, if with a few straight black setae, the stems and petioles not setose; achenes distinctly or strongly ribbed.
 - E Largest heads of the inflorescence with 5-7 inner involucral bracts; 5-10-flowered.
 - F Involucral bracts with a glabrate median part, conspicuously white-tomentose near the scarious margins; achenes reddish or brownish, shorter than the pappus, strongly ribbed; cauline leaves generally much reduced or absent; inflorescence usually branching from the middle of the stem or below, with 7-40 (mostly 15-30) heads in well-developed plants.....119. *C. pleurocarpa*, p. 589
 - FF Involucral bracts glabrous or sparingly and evenly tomentulose, the inner ones yellowish-green, shading indistinctly into the scarious margins; achenes yellow, buff, or tawny, equal to or longer than the pappus, finely ribbed; cauline leaves, at least 1-3, well developed, inflorescence branching from the upper half of the stem, with 15-200 (mostly 30-100) heads in well-developed plants....120. *C. acuminata*, p. 592
 - EE Largest heads of the inflorescence with 8-13 inner bracts; 9-40-flowered.

- G Achenes deep or pale green, strongly attenuate toward the apex or substrate; lobes of the leaves linear or narrowly lanceolate, 0.5–2.5 mm wide, falcate, mostly entire.....121. *C. atribarba*, p. 595
- GG Achenes yellowish or brownish, slightly or moderately attenuate toward the apex; lobes of the leaves broadly lanceolate or deltoid, or, if narrower, generally toothed or lobed.
- H Plants mostly 1–3 dm high, bearing a cymose inflorescence of 2–25 heads; involucre broadly cylindric, 5–9 mm wide at anthesis, 9–40 (mostly 12–25)-flowered; longest outer bracts mostly $\frac{1}{3}$ – $\frac{2}{3}$ as long as the inner bracts.
- I Leaves grayish tomentose, not gland-pubescent; peduncles not expanded toward the apex...116. *C. occidentalis*, p. 576
- II Leaves green, gland-pubescent, in fresh specimens with a conspicuous reddish midrib and petiole; peduncles expanded toward the apex.....117. *C. Bakeri*, p. 581
- HH Plants mostly 2.5–6 dm high, bearing an ample cymose panicle of 20–60 heads; involucre narrowly cylindric, 3–5.5 mm wide at anthesis, 7–15 (mostly 8–10)-flowered; longest outer bracts mostly $\frac{1}{5}$ – $\frac{1}{3}$ as long as the inner bracts.
- J Involucres glabrous120. *C. acuminata* subsp. *pluriflora*, p. 594
- JJ Involucres tomentulose or tomentose.
- K Basal leaves glabrate; involucre bracts glabrate on the median part, strongly tomentose near the scarious margins119. *C. pleurocarpa* (fa. apm. *plumaensis*), p. 591
- KK Basal leaves grayish tomentose; involucre bracts evenly tomentose or tomentulose...112. *C. intermedia*, p. 599

115. *Crepis monticola* Coville

Contr. U. S. Nat. Herb. 3: 562. 1896. (Fig. 166.)

Perennial, 1.3–3.5 dm high, the stems, leaves, and involucre sparsely tomentulose and (except in apm. *calva*) densely hirsute with long, glandular hairs; rootstock vertical, woody, elongated into the strong taproot, crowned with the leafy simple or 1-furcate caudex; caudical leaves 10–25 cm long, 2–4 cm wide, elliptic or oblanceolate, acute, mostly pinnatifid with lanceolate acuminate dentate lobes, or sometimes merely dentate or rarely denticulate, attenuate into a long-winged petiole, becoming stramineous toward the base; cauline leaves several, the lower resembling the caudical ones, the others gradually reduced, elliptic, oblong or lanceolate, acuminate, mostly rather broad-based, often \pm auriculate; stem erect, stout, or sometimes slender and flexuous, sulcate or striate, several-branched beginning usually near the base, the branches strict, 1–6-headed; peduncles 1–8 cm long, rather stout, somewhat thickened near the head in fruit; inflorescence cymose, of 2–20 heads; heads erect, large, 16–20-flowered; involucre campanulate, 14–24 (mostly over 18) mm long, 5–10 mm wide at middle; outer bracts 3–10, the longest $\frac{1}{2}$ – $\frac{3}{4}$ as long as the inner, narrowly lanceolate or linear, acuminate; inner bracts 7–12, lanceolate, long-acuminate (except in apm. *plumaensis*), densely strigulose on inner face with yellowish shining trichomes, becoming narrowly carinate dorsally, carina yellowish, spongy-thickened; receptacle areolate, glabrous; corolla 16–21 mm long; ligule 3–3.5 mm wide; teeth 0.4–1 mm long, gland-hooded; corolla tube about 6 mm long, pubescent with stout acicular trichomes often in clumps; anther tube (5)7 \times 1.75(2) mm dis.; appendages 0.5–1 mm long, oblong, acute or truncate; style branches 2–3.5 mm long, 0.25 mm wide, yellow; achenes reddish-

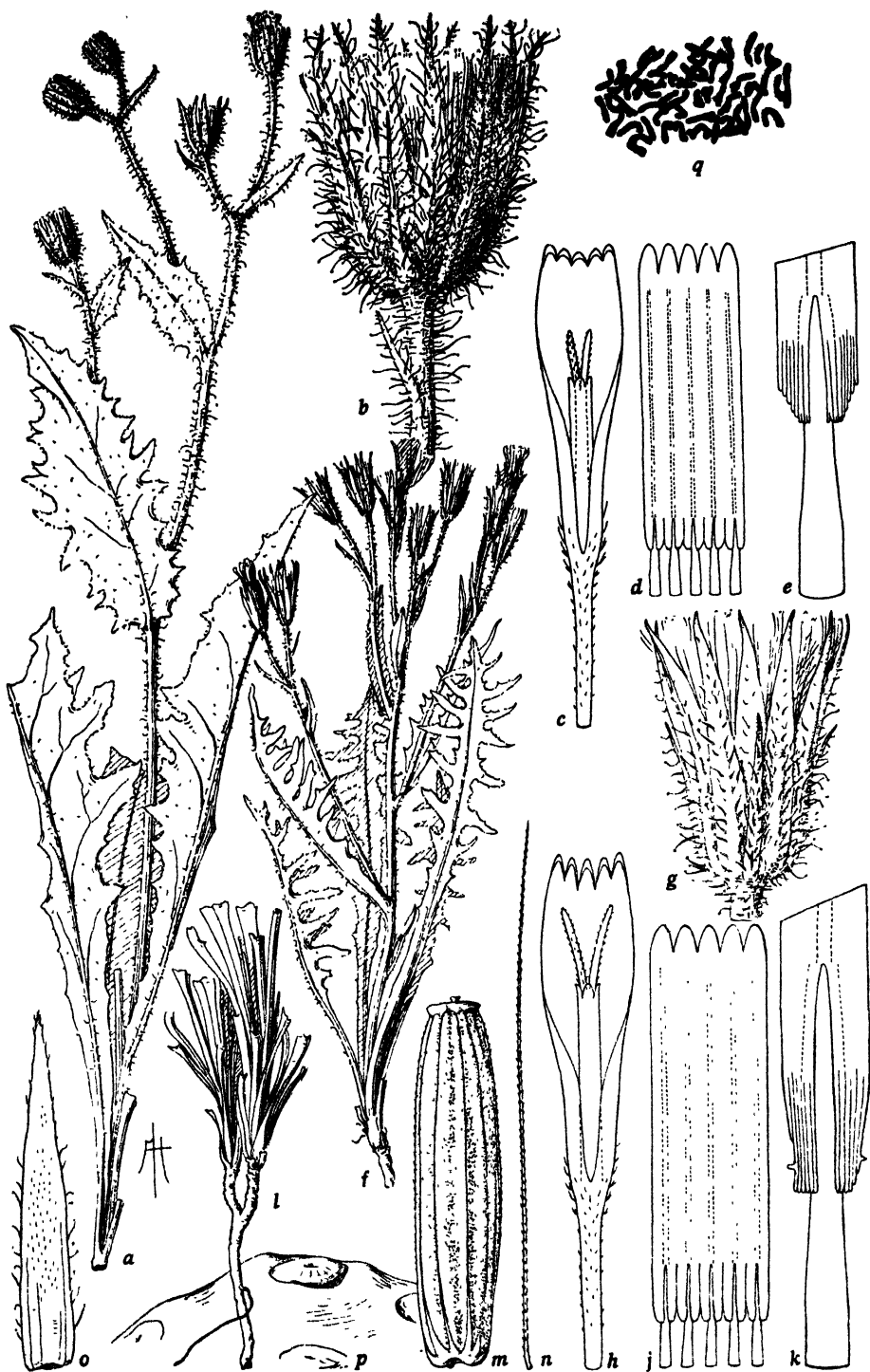


Fig. 166. *Crepis monticola*, a-e, diploid form, from Butler in 1910 (UC 163935); f-k, apm. *australis*, from Hall 9532 (UC 174026); l-q, apm. *plumaeensis*, from Babcock and Navashin 183 (UC 346534): a, plant, $\times \frac{1}{2}$; b, fruiting head, $\times 2$; c, floret lacking ovary, $\times 4$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, plant, $\times \frac{1}{2}$; g, fruiting head, $\times 2$; h, floret lacking ovary, $\times 4$; i, anther tube, $\times 8$; j, detail of appendages, $\times 32$; k, detail of appendages, $\times 32$; l, base and root of plant, $\times \frac{1}{2}$; m, n, achene and pappus seta, $\times 8$; o, inner involucre bract, inner face, $\times 4$; p, detail of receptacle, $\times 25$; q, somatic chromosomes, $2n = 55$ ♀, $\times 1250$.

brown, 5.5–9 mm long, about 1.5 mm wide, fusiform, usually more attenuate to the apex, with paler pappus disk, somewhat constricted at the strongly calloused base, about 13-ribbed, the ribs strong or very strong, sometimes with 3–4 weaker, smooth or finely spiculate under lens; pappus white or pale cream, 9–13 mm long, 4–5-seriate, the setae unequal, outermost shorter and finer, the coarsest up to 50μ (5 cells) wide at base, stiff but pliable, persistent. Flowering May–July; flowers yellow. Chromosomes, $2n = 22$!, 33 ?, 44 !, 55 ?, 77 ?, or 88 ?

Crepis occidentalis var. *crinita* Gray, Bot. Cal. 1: 435. 1876; Syn. Fl. 1(2): 432. 1884, with respect to California plants.

S. Oregon and N. California, south in the Sierra Nevada to Sierra Co., and in the Coast Ranges to Lake Co. and Mt. Hamilton.

C. monticola is the most restricted in range of all the indigenous American species of *Crepis*. The original diploid form occurs only in the valleys and lower foothills of central Siskiyou Co., California; but there it is rather abundant and sometimes occurs in coniferous forests. Apomictic polyploid forms essentially similar to, and probably directly derived from, this original diploid form occur with it and for some distance to the north and south. Other apomictic polyploid races, more or less transitional to either *C. occidentalis*, *C. pleurocarpa*, or *C. modocensis*, extend the range south and east to the western edge of the Great Basin. For a key to 10 apomictic forms and citation of specimens under each, consult Babcock and Stebbins (B. and S., 504: 115–118). Only specimens of the diploid form are cited below.

California: Siskiyou Co., near Yreka, *Butler 750* (UC, DS); south of Yreka, 810 m, *Babcock and Stebbins 1887, 1888, 1928* (UC); N.E. side of Scott Valley, 900 m, *Stebbins and Jenkins 2442* (UC). Etna, *Eastwood and Howell 5032* (CA); near Mt. Shasta, *Babcock and Stebbins 1973, 1974* (UC); Trinity Co., north of Carrville, summit of Scott Mts., *Howell 13689* (UC, CA).

Relationship

C. monticola is strikingly distinct from all the other native American *Crepis* in its dense indumentum of long gland hairs and especially in its long-attenuate inner involucre bracts which do not cover the florets in the unopened heads. As was stated by Babcock and Stebbins (*op. cit.*, p. 30), the existing Asiatic species showing most similarity to *C. monticola* are *C. kashmirica* and *Dubyaea hispida*, both of the Himalayan reg. It is probable, therefore, that the ancestors of *C. monticola* were among the oldest, most primitive members of the genus. It is also probable (*op. cit.*, p. 32) that, before the hybridization that produced *monticola* had occurred, these ancestors had migrated northeastward from Central Asia into E. Siberia at a time when a cool, subhumid to semiarid climate prevailed in that region, at least in the lowlands. These two ancestral species must have had either 5 and 6 or 4 and 7 pairs of chromosomes, respectively. It may be assumed that hybridization occurred in E. Siberia and that the derived amphidiploid form (the original 22-chromosome *C. monticola*) migrated across "Beringea" into North America. Then the ancestral species, as well as the amphidiploid hybrids that remained in Asia, were apparently all exterminated, probably during the Pleistocene age.

116. *Crepis occidentalis* Nutt.

Jour. Acad. Phila. 7: 29. 1834. (Fig. 167.)

Perennial, 0.8–4 (mostly 1.5–2.5) dm high, the stems, leaves, and involucre covered with a close gray tomentum (this often thin and falling with age), often gland-pubescent above, especially on the peduncles, sometimes with black glandular setae especially on the involucre; root slender, elongated, arising from a deeply penetrating thicker taproot; caudex somewhat swollen, leafy or covered with the

brown remnants of old leaf bases; caudical leaves rather thick, 8–35 cm long, 2–6 cm wide, elliptic, acute or acuminate, sinuately dentate or runcinately or deeply pinnatifid with lanceolate or linear toothed lobes, attenuate into a long or short winged petiole, becoming stramineous near the base; cauline leaves similar, gradually reduced, the upper sessile, subamplexicaul, uppermost linear, entire; stems 1–3 from each caudex, erect, stout, sulcate or striate, several-branched above or beginning near the base, the branches strict, 1–20-headed, forming a simple few-headed or compound many-headed corymbiform cyme; peduncles 1–6 mm long, stout, slightly thickened near the head in fruit; heads erect, mostly large, 9–40-flowered; involucre cylindric-campanulate, 11–19 mm long, 5–10 mm wide at middle; outer bracts 6–8, the longest about $\frac{1}{3}$ or rarely $\frac{1}{2}$ as long as the inner, triangular, lanceolate or linear; inner bracts 7–18, lanceolate, acute or acuminate, strigulose, finely pubescent or glabrous on inner face, becoming dorsally carinate toward the base at maturity, carina brownish, spongy-thickened; receptacle areolate or pitted, glabrous or very shortly ciliate; corolla (in diploid form) about 22 mm long; ligule 2.5–3 mm wide; teeth 0.4 mm long; corolla tube 9–10 mm long, pubescent with short coarse 2-celled acicular hairs; anther tube about 6 x 2 mm dis.; appendages 0.7 mm long, oblong, acute; filaments 0.5 mm longer; style branches 3.5 mm long, 0.25 mm wide, yellow; achenes from light to very dark brown, 6–10 mm long, about 1.5 mm wide, slightly attenuate at the apex or tapering to 0.5 of the width at the middle, strongly calloused at the base, sometimes with paler pappus disk, 10–18-ribbed, the ribs very strong, rounded, finely spiculate under lens; pappus dusky or yellowish-white, 10–12 mm long, 4–6-seriate, the setae united at the base and coming away in clumps, unequal, the outermost shortest and finest, the coarsest about 50μ (5–6 cells) wide at the base, persistent. Flowering June–July; flowers yellow. Chromosomes, $2n = 22!$, $33!$, $44!$, $55!$, $66!$, $77!$, $88!$

Saskatchewan and Montana west to British Columbia, and south to New Mexico, Arizona, and S. California.

One of the most widespread of the American species of *Crepis*, *C. occidentalis* is second only to *C. runcinata* in polymorphism. The many local apomicts of *C. occidentalis* fall into 4 morphologically distinct groups which differ in their geographic ranges. These groups of forms are recognized as subspecies; and one of them, subsp. *typica*, includes the diploid forms.

Key to the Subspecies of C. occidentalis

Involucres with at least some glandular pubescence.

Involucres, peduncles, and upper cauline leaves slightly or strongly glandular but not setose; largest heads of the inflorescence with 10–13 inner bracts, 18–30-flowered. . . 116, *a. typica*

Involucres, peduncles, and generally the upper cauline leaves bearing conspicuous glandular setae; largest heads of the inflorescence with 8 inner bracts, 12–14-flowered. 116, *b. costata*

Involucres completely devoid of glandular pubescence; or if with a few gland hairs, the involucres with 8 inner bracts and less than 15 florets.

Stems well developed, 1–4 dm high, with a definite primary axis; involucres mostly with 8 inner bracts and with the outer bracts about $\frac{1}{3}$ as long as the inner; leaves, if pinnatifid, with closely spaced, strongly toothed or pinnatifid lobes. 116, *c. pumila*

Stems low, 0.5–2 dm high; inflorescence branching from near base of stem, bearing heads mostly on long, divergent peduncles; involucres with 8–12 inner bracts and with the outer bracts $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner; leaves deeply pinnatifid, with remotely spaced, lanceolate, entire or coarsely few-toothed lobes. 116, *d. conjuncta*

116, *a. Crepis occidentalis typica* Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 120. 1938. Plant 1–4 dm high; leaves very variable in size and degree of dissection; inflorescence composed of about 10–30 heads; peduncles usually gland-

pubescent; involucre broadly cylindric or cyathiform, the bracts densely or sparsely glandular; inner bracts 8–13, always at least 10 on the largest heads; florets 12–30 per involucre, 18 or more in the larger ones; achenes mostly medium brown, with moderately strong ribs. See fig. 167, *a–g*.

Crepis occidentalis Nutt., *loc. cit.*

Psilochaenia occidentalis Nutt., Trans. Am. Phil. Soc. n.s. 7: 436. 1840, in part.

Hieraciodes occidentale O. Kuntze, Gen. 1: 346. 1891.

Common in California, W. Nevada, and S. Oregon; becoming rare in central, N., and E. Oregon and S.E. Washington; occasional in Idaho, W. Wyoming, Utah, Colorado, and New Mexico; not seen from Montana, E. Wyoming, or the Great Plains reg.

This subspecies includes the diploid forms, which represent the original stock of *C. occidentalis*, and certain polyploid forms. The diploid forms are confined to N. and E. California and adjacent Nevada. Within this area and extending from it in different directions, are numerous polyploid forms, most or all of which are partly or wholly apomictic. A few of these are morphologically identical with the diploid forms, except for the larger size of all their parts; but most of them verge toward some one of the other subspecies or toward other species of *Crepis*. For a key to these forms and citation of specimens under each see Babcock and Stebbins (*op. cit.*, 121–124). The specimens cited below comprise diploid forms only.

California: Sierra Co., northwest of Sierraville, 1600 m, *Babcock and Navashin 168* (UC); Plumas Co., Feather River Inn, *Babcock 157* (UC); Lassen Co., ridge east of Red Rock (Constantia), *Babcock and Stebbins 1748* (UC); Siskiyou Co., Montague, *Smith 696* (G, CA). **Nevada:** Washoe Co., Reno, *Kennedy* in 1901 (UC); west of Reno, *Stebbins and Jenkins 2185* (UC).

116, *b. Crepis occidentalis costata* (Gray) Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 124. 1938. Plant 0.8–4 dm high; leaves mostly pinnatifid; involucre, peduncles, and often the upper cauline leaves bearing dark, or sometimes pale, gland-tipped setae; inflorescence mostly of 15–30 heads; involucre narrower than in subsp. *typica*, with 7–8 inner bracts and 10–14 florets; achenes often darker and more strongly ribbed than in subsp. *typica*. See fig. 167, *h–m*.

Crepis occidentalis var. *costata* Gray, Bot. Calif. 1: 435. 1876.

Psilochaenia occidentalis Nutt., *loc. cit.*, in part.

C. grandifolia Greene, Pittonia 3: 107. 1897.

Throughout the N. half of the range of the species, and in this area the most common group of forms; south to Colorado, Utah, and N. California.

This subspecies, as here recognized, is a series of polyploid, presumably apomictic races which, in their few-flowered heads and frequently reduced outer involucre bracts, are definitely transitional toward *C. intermedia*. They also show affinity with *C. Bakeri* in their strong glandular pubescence and, in most forms, their deeply pinnatifid and toothed leaves, although other races of subsp. *costata* are in this respect nearer to subsp. *typica*. For a key to 8 polyploid forms and citations of specimens under each, see Babcock and Stebbins (*op. cit.*, 126–128). The specimens cited below all represent apm. *Grayi*, which, like most of the forms comprising this subspecies, combines certain features of 3 different species, viz., *C. occidentalis*, *C. Bakeri*, and *C. acuminata*.

Utah: Great Salt Lake, Stansbury Island, 1300 m, *Watson 715* (G) type of *C. occidentalis* var. *costata* Gray; Salt Lake City, *Garrett 1829* (DS); *ibid.*, *Garrett* in 1926 (UC). **Idaho:** Shoshone, *Palmer 140* (DS, G, Clo).

116, *c. Crepis occidentalis pumila* (Rydb.) Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 128. 1938. Plant 1–4 dm high, often slender and few-headed

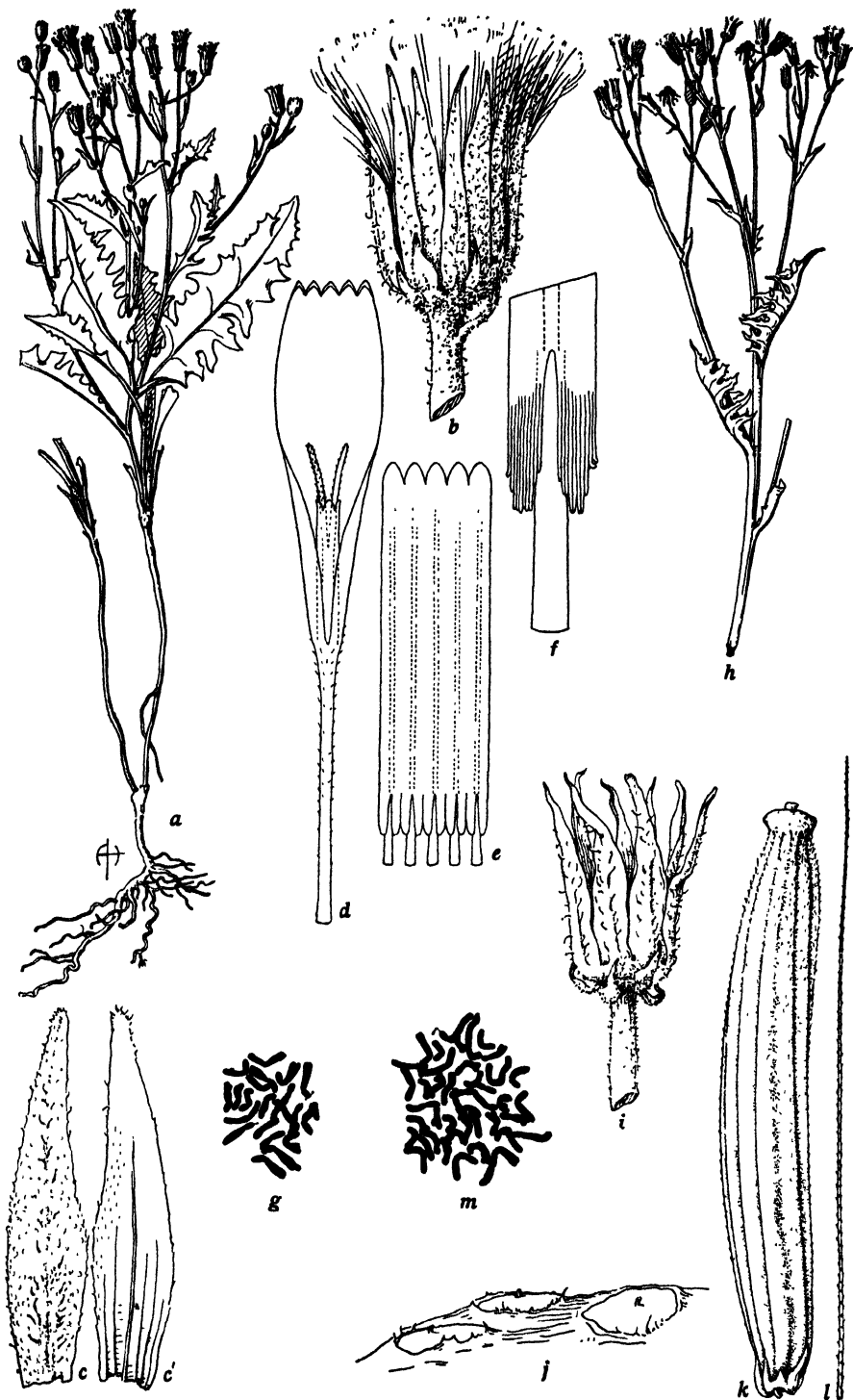


Fig. 167. *Crepis occidentalis*, a-g, subsp. *typica*, diploid form, from Babcock and Navashin 168 (UC 346549); h-m, subsp. *costata* apm. Grayi, from Garrett in 1926 (UC 346590): a, plant, $\times \frac{1}{4}$; b, head, $\times 2$; c, σ , inner involucre bract, outer and inner face, $\times 4$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, somatic chromosomes, $2n = 22$, $\times 1250$; h, plant, $\times \frac{1}{4}$; i, head, $\times 2$; j, detail of receptacle, $\times 25$; k, l, achene and pappus seta, $\times 8$; m, somatic chromosomes, $2n = 44$, $\times 1250$.

but sometimes robust and many-headed, completely devoid of glandular pubescence (except in apm. *olympica*); leaves variable; involucre narrower than in subsp. *typica* with mostly 8 inner bracts and 12–20 florets; achenes as in subsp. *typica*.

Crepis pumila Rydb., Mem. N. Y. Bot. Gard. 1: 462. 1900.

Range of the species in California, W. Nevada, and S. Oregon, and locally in the mountains of Montana, Idaho, and Washington.

The group of forms comprising this subspecies is in general transitional from subsp. *typica* toward *C. intermedia*; i.e., they are *C. occidentalis* with an admixture of *C. acuminata* or *C. pleurocarpa*. Some of the forms are nearly identical with the taller forms of subsp. *typica*, from which they differ only in their complete lack of glandular pubescence and their tendency toward fewer bracts and florets; but these merge into a series of intermediate forms which in habit and floral characters are similar to the larger-headed forms of *C. intermedia*. The dwarf forms of this subspecies, including that represented by the type and those found in S. California, show in their leaf shape, habit, and sometimes their involucre, an admixture of *C. modocensis* (or possibly *C. Bakeri*); but no clear dividing line, either morphologically or geographically, can be drawn between these and the tall robust forms most common in N. California. For a key to 10 apomicts and citation of specimens of each, see Babcock and Stebbins (*op. cit.*, 130–134). Only apm. *Rydbergii* (represented by the type of *C. pumila*) and some closely related forms from California and Nevada are cited here.

Montana: Bridger Mts., 2100 m, *Rydberg and Bessey 5305* (NY) type of *C. pumila* Rydb.

California: Siskiyou Co., Mt. Shasta, Sheep Rock, 1500 m, *Hall and Babcock 4116* (UC, DS); Plumas Co., Round Lake, 2000 m, *Head* in 1921 (CA); Ventura Co., Frazier Mt., *Hall 6595* (UC, DS, RM). **Nevada:** Charleston Mts., Kyle Canyon, 2570 m, *Jaeger* in 1926 (UC).

116, *d. Crepis occidentalis conjuncta* (Jepson) Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 134. 1938. Plant 0.5–2 dm high, the stems few-branched beginning near the base, the branches arcuate; lower leaves 10–18 cm long, pinnatifid, the segments remote, lanceolate or sometimes nearly linear, salient or retrorse, entire or remotely and acutely dentate; heads 2–9, mostly on long peduncles, with 12–30 florets; involucre tomentulose, neither glandular nor setose; outer bracts $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner; inner bracts 8–12; achenes as in subsp. *typica*.

Crepis occidentalis var. *conjuncta* Jepson, ex Babcock et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 134. 1938.

C. occidentalis var. *nevadensis* Kellogg, Proc. Cal. Acad. Sci. 5: 50. 1873 in part (†); Gray, Syn. Fl. 1(2): 432. 1884.

Sierra Nevada and other mountains of N. California and S. Oregon, where it passes into subsp. *pumila*; mountains of S.E. Washington and N.W. Wyoming.

This distinct subspecies combines the habit and longer outer involucral bracts of *C. Bakeri* or *C. modocensis* with a leaf shape most characteristic of *C. modocensis*, but with the indumentum and achene characters of *C. occidentalis pumila*. This subspecies also differs in habitat from the other subspecies of *C. occidentalis*. It occurs most often in forested areas with a relatively high precipitation. In the Sierra Nevada it is locally frequent on the W. slope at middle altitudes, where it is often the only form of *Crepis* found, the others occurring mostly in open valleys or on the brush-covered hills on the E. side of these mountains. For a key to 4 apomictic forms and citation of specimens of each, see Babcock and Stebbins (*op. cit.*, 135–138). The specimens cited below represent apm. *pluriflora*, which apparently combines characteristics from *C. occidentalis*, *C. modocensis*, *C. Bakeri*, and possibly *C. pleurocarpa*.

California: Placer Co., Cisco, Camp Yuba, Kellogg, June 18, 1870 (UC 31318, US, G, DS) type and isotypes of subsp. *conjuncta*; Nevada Co., Soda Springs, 2120 m, Jones in 1881 part (Po); Alpine Co., Dardanelles Mt., 2200 m, Eggleston 9943 (US); Placer Co., Deer Park, Geis 33 (UC); Placer Co., Tahoe City, Eastwood 460 (CA, Clo); Nevada Co., Truckee, Sonne in 1884 (UC); Nevada Co., Hobart Mills, Drew in 1925 (DS); Plumas Co., Gray Eagle resort, Babcock 153, 154 (UC).

Relationship

Crepis occidentalis, by virtue of the dense gray tomentum on the younger leaves and involucre, is a well-marked species. An Old World species which resembles it in this respect, as well as in involucre characters, is *C. oreades*, a 4-paired species now occurring in the mountains of Central Asia. A possible other parental species, with 7 pairs of chromosomes, is *C. flexuosa*, also of Central Asia. Both of these species are distributed rather widely in that region at present, and it is not unlikely that they or similar species occurred farther to the east in the Tertiary period.

117. *Crepis Bakeri* Greene

Erythca 3: 73. 1895. (Fig. 168.)

Perennial, 0.8–3 dm high, with dark green gland-pubescent leaves, stems and involucre, the stems and midribs of the leaves often deep reddish-purple; root slender, elongated; caudex slightly swollen, covered with brown or stramineous bases of old leaves; caudical leaves 8–20 cm long, 2–5 cm wide, elliptic, acute, mostly deeply pinnatifid with lanceolate or narrowly elliptic dentate segments, occasionally runcinate-dentate, attenuate into a long or short winged petiole, canescent-tomentulose or glabrate; cauline leaves similar or acuminate, the upper sessile, sub-amplexicaul, uppermost linear, entire; stems 1–3 from each caudex, erect, stout, remotely several-branched beginning near the base or above the middle, striate or sulcate; branches stout, strict or arcuate, 1–4 headed, forming a 2–22-headed cyme; peduncles 1–9 cm long, stout, becoming definitely broader toward the head; heads erect, large, with 11–40 or more florets; involucre 11–21 mm long, 5–15 mm wide at middle; outer bracts 8–10, unequal, the longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner, lanceolate, acuminate; inner bracts 10–14, lanceolate, acute or acuminate, glabrous or sparsely pubescent on inner face, becoming narrowly carinate dorsally, sometimes without much change in color, becoming spongy-thickened toward the base at maturity; receptacle areolate, pitted, glabrous; corolla about 20 mm long; ligule 3 mm wide; teeth 0.25–0.75 mm long; corolla tube 6 mm long, pubescent with very short stout pointed hairs; anther tube 7×2 mm dis.; appendages 1 mm long, lanceolate, fringed at apex; filaments 1 mm longer; style branches 2 mm long, 0.25 mm wide, yellow; achenes dark or pale brown or yellowish, 6–10.5 mm long, about 1.5 mm wide. \pm attenuate to the apex, with slightly expanded paler pappus disk, somewhat narrowed to the strongly calloused base, about 13-ribbed, the ribs rather strong, rounded, smooth or finely spiculate under lens; pappus dusky or yellowish-white, 6–13 mm long, 4-seriate, the setae unequal, outermost shortest and finest, the coarsest about 50μ (5 cells) wide at base, persistent. Flowering May–July; flowers yellow. Chromosomes, $2n = 22!$, $33!$, $44!$, $55!$

Central Washington and E. Idaho locally, south through central Oregon to N. California. Like *C. monticola* and *C. modocensis*, this is a montane species in contrast with *C. occidentalis*, which occurs more generally on lower slopes and valley terraces. It is found in more arid, less heavily wooded areas than *C. monticola*, but usually not in as exposed situations as *C. modocensis*, although it often grows together with the latter in the region around Sierra Valley and southwest of Honey Lake in the N. Sierra Nevada.

Three subspecies, *typica*, *Cusickii*, and *idahoensis*, have been recognized.

Key to the Subspecies of *C. Bakeri*

Involucres broadly cylindric or cyathiform; outer bracts lanceolate, the longest about $\frac{1}{2}$ as long as the inner; pappus about equal to or shorter than the achenes.

Involucres in flowering heads 14–17 mm, in fruit 16–20 mm long; pappus at anthesis 9–10.5 mm long; achenes 8–10.5 mm long, usually less strongly attenuate at the apex.....117, *a. typica*

Involucres in flowering heads 10–15 mm, in fruit 13–17 mm long; pappus 6–9 mm long; achenes 6–9 (10) mm long, usually more strongly attenuate at the apex. 117, *b. Cusickii*

Involucres narrowly cylindric or turbinate, 18–21 mm long in fruit; outer bracts deltoid, the longest $\frac{1}{8}$ – $\frac{2}{5}$ as long as the inner; pappus longer than the achenes.....117, *c. idahoensis*

117, *a. Crepis Bakeri typica* Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 139. 1938. Plant size, habit, leaves, and florets as described above for the species; inflorescence of 2–13 (19) heads; involucres broadly cylindric or cyathiform, 16–20 mm long in fruiting heads; outer bracts lanceolate, the longest about $\frac{1}{2}$ as long as the inner; achenes 8–10.5 mm long, mostly only slightly attenuate at the apex; pappus on mature achenes 9–10.5 mm long, about equal to the achenes. See fig. 168, *f–j*.

Crepis Bakeri Greene, *loc. cit.*

Range of the species, except Idaho.

This subspecies contains only polyploid forms, most of which are apparently tetraploid. No apomictic forms could be recognized with certainty, perhaps because the degree of variation within the subspecies is relatively slight, perhaps because the collections are from too widely scattered localities, and possibly because apomixis is less strongly developed in this species. The following are a few of the specimens seen.

California: Modoc Co., Egg Lake, *Baker and Nutting* in 1893 (UC) photograph of type of *C. Bakeri*; Placer Co., Summit, *Eastwood* in 1898 (CA); Sierra Co., Sardine Peak, S. slope along Lemmon Canyon road, gravelly soil with *Artemisia* and *Wyethia*, *Babcock* 141–143 (UC); Plumas Co., Beckwith Peak, 1700 m, *Stebbins and Jenkins* 2149 (UC). **Nevada:** Hunter Creek, Dinsmore camp, 1820 m, *Kennedy* 1634 (UC, DS, US). **Oregon:** Jackson Co., Kean Creek, 1550 m, *Apple-gate* 2300 (DS, US); Crook Co., Grizzly Butte, 1250 m, *Leiberg* 219 (UC, US). **Washington:** Klickitat Co., *Suksdorf* 875 (UC, US); Kittitas Co., north of Ellensburg, 550 m, *Keck and Clausen* 3530 (UC).

117, *b. Crepis Bakeri Cusickii* (Eastw.) Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 140. 1938. Similar to subsp. *typica*, but smaller throughout; inflorescence of 1–10 heads; involucres in flowering heads 10–15 mm long, in fruiting heads 13–17 mm long; mature achenes 6–9 (10) mm long, mostly strongly attenuate at the apex; pappus 6–9 mm long. See fig. 168, *a–e*.

Crepis Cusickii Eastwood, Bull. Torr. Bot. Club 30: 503. 1903.

N. California and S. Oregon.

This subspecies contains diploid forms as well as forms which are apparently triploid but are morphologically indistinguishable from the former. It is distinguished from subsp. *typica* by few characteristics except for the smaller size of both its vegetative and floral parts; but, since these differences are associated with a relatively restricted geographic range, its recognition seems warranted.

California: Siskiyou Co., north of Hornbrook, *Collins* in 1927, also cult. as hort. genet. Calif. no. 2220 (UC) ($2n = 22!$); Siskiyou Co., Yreka, *Smith* 699 (US, CA) diploid (!); Siskiyou Co., Hilt, *Smith* in 1915 (US, CA) triploid (!); Lassen Co., between Bogard Ranger Station and Harvey Valley, 1630 m, *Stebbins and Jenkins* 2331 (UC) ($2n = 22!$); Lassen Co., north of Susanville, *Gillespie* 9337 (DS) triploid (!); Lake Co., south of Bulls Prairie, *Loveless* 146 (UC) diploid (!). **Oregon:** 15 miles east of Ashland, 1200 m, *Cusick* 2872 (UC, DS, G, Po, Minn) type

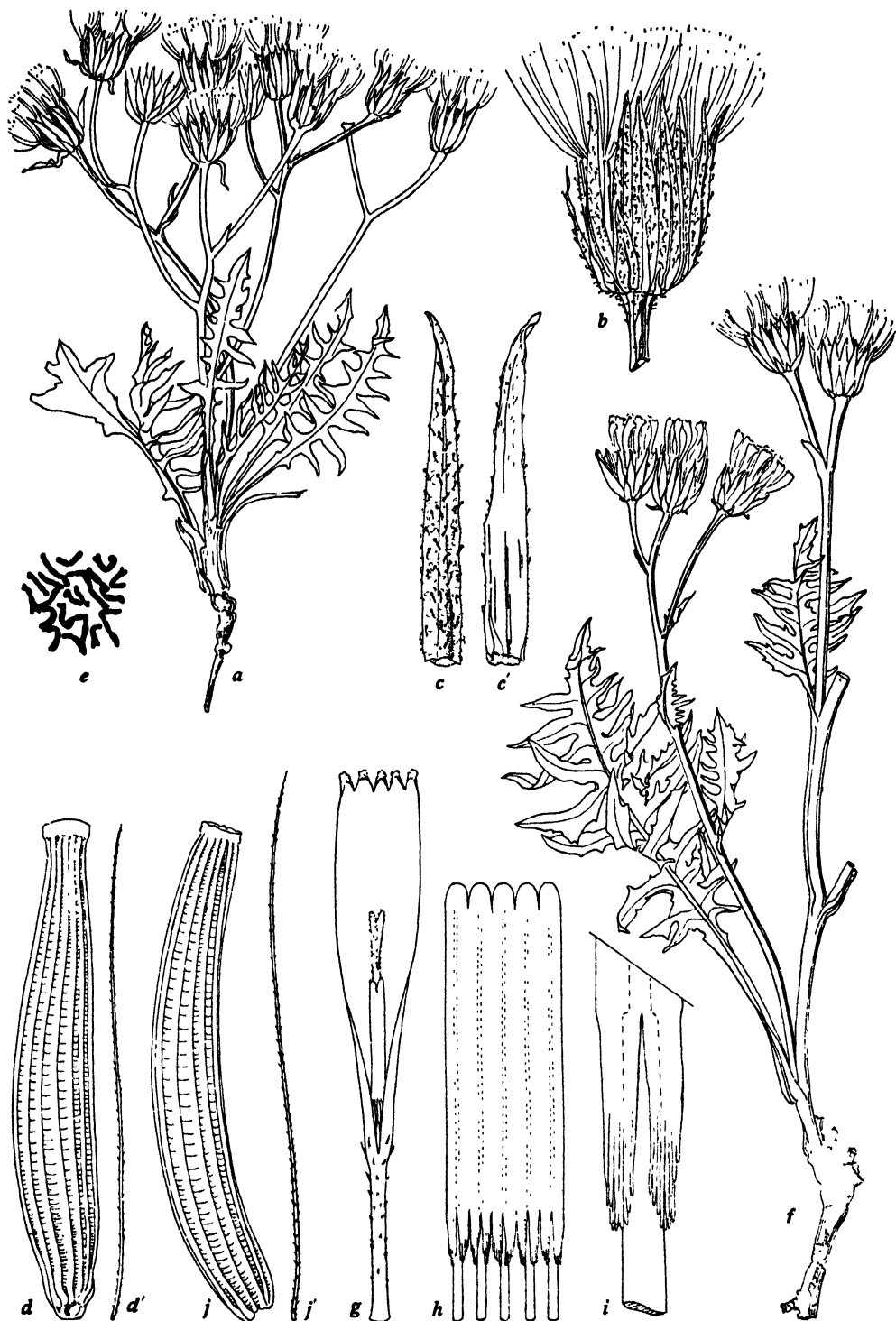


Fig. 168. *Crepis Bakeri*, a-e, subsp. *Cusiokii*, diploid form, a-d, from Collins in 1927 (UC 313842); e, from Stebbins and Jenkins 2331 (UC 581287); f-j, subsp. *typica* (polyploid, $4n ?$), from Babcock 141 (UC 346507): a, plant, $\times \frac{1}{2}$; b, fruiting head, $\times 2$; c, c', inner involucral bract, $\times 4$, showing dorsal keel, spongy-thickening near base, and hairs on inner face; d, achene and pappus seta, $\times 8$; e, somatic chromosomes, $2n = 22$; f, part of plant, $\times \frac{1}{2}$; g, floret lacking ovary, $\times 4$; h, anther tube, $\times 8$; i, appendages, $\times 32$; j, achene and pappus seta, $\times 8$.

collection of *C. Cusickii*, triploid (♀); Jackson Co., Siskiyou Mts., along Pacific highway, *Henderson 12910* (UC) triploid (♀).

117, c. ***Crepis Bakeri idahoensis*** Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 141. 1938. Plant 2.5–3 dm high; caudical leaves 15–18 cm long, 5–5.5 cm wide, shallowly pinnatifid with deltoid dentate lobes; cauline leaves similar, the lobes strongly mucronate; inflorescence of 11–22 heads; peduncles conspicuously expanded toward the head; heads large, 18–25-flowered; involucre 18–21 mm long in fruiting heads; outer bracts deltoid, acute or acuminate, the longest $\frac{1}{3}$ – $\frac{2}{5}$ as long as the inner; inner bracts 8–13, lanceolate or linear; achenes chestnut brown, about 8 mm long, rather strongly contracted toward the apex; pappus 12–13 mm long. Chromosomes, $2n = 55$ ♀

Idaho: Nez Perces Co., Clearwater R. valley, *Sandberg, MacDougal and Heller 268* (G, Minn, RM) type collection; Nez Perces Co., Culdesac, *Warren* in 1932 (WSC); Nez Perces Co., Lake Waha, *Henderson* in 1894 (RM); Nez Perces Co., Lewiston, 400 m, *Hitchcock and Samuel 2533* (RM, CA); *ibid.*, Lewiston Hill, treeless arid transition zone, *Sharsmith 3549* (UC).

This subspecies, although represented by specimens from only a restricted region, is so strikingly different from any other forms of either *C. Bakeri* or *C. occidentalis* that it deserves recognition. In leaf shape it approaches *C. occidentalis*, but the absence of dense tomentum, the glandulosity and the swollen peduncles are characteristic of *C. Bakeri*. Also it differs from the only forms of *C. occidentalis* occurring in that vicinity in its much more numerous inner bracts and florets. In the shape of its involucre, inner bracts, and achenes it suggests *C. monticola*. It is apparently an allopolyploid derivative of complex origin, involving *C. Bakeri*, *C. occidentalis*, and probably *C. monticola*. The specimens from Lake Waha and Culdesac belong to the same apomictic form as the type, whereas that from Lewiston differs in its less attenuate inner bracts, and is therefore transitional toward *C. occidentalis costata*.

Relationship

Crepis Bakeri resembles *C. occidentalis* in the size, shape, and ribbing of the achenes, but it differs not only in its green, sparingly tomentose leaves with conspicuous reddish midribs, but also in its fewer-headed inflorescence and the inflated peduncles. In shape of leaves, habit of branching, and shape of involucre, it suggests *C. modocensis*; whereas in its glandular indumentum and inflated peduncles it approaches *C. monticola*. As stated above, its ecological requirements are intermediate between those of *C. monticola* and *C. modocensis*. It was suggested by Babcock and Stebbins (*op. cit.*, p. 31) that the widespread Asiatic species, *C. Bungei*, exhibits sufficient similarity to *C. Bakeri* to warrant its consideration as the 4-paired ancestor of *C. Bakeri*. It was also noted that *C. Bakeri Cusickii*, which includes the diploid form, sometimes occurs on moist meadows and valley flats, thus recalling the habitat of *C. Bungei*. It is probable that the 7-paired ancestor of *C. Bakeri* is now extinct, but it may have been a close relative of *C. flexuosa*.

118. ***Crepis modocensis*** Greene

Erythea 3: 48. 1895. (Figs. 169, 170.)

Perennial, 0.5–4.5 dm high, the stems glabrate or tomentose, the basal part or occasionally the whole stem with scattered glandless setae; root slender, elongated, woody; caudex swollen, simple or 2–4-furcate, covered with brown bases of old leaves; caudical leaves 7–25 cm long, 1–7 cm wide, elliptic, acute or acuminate, deeply pinnatifid with lanceolate dentate segments or bipinnatifid, the ultimate segments or teeth acute and corneous-mucronate, attenuate into a long petiole,

becoming broader and stramineous toward the base, glabrate or tomentose and generally setose along the petiole and midrib; cauline leaves similar, the upper sessile, uppermost linear, entire; stems 1–4, erect, slender to stout, terete, striate, simple, 1-furcate or cymosely branched, the inflorescence comprising 1–10 heads; peduncles 1.5–13 cm long, stout, strict, expanded near the head in fruit; heads erect, medium to large, 10–60-flowered; involucre cylindric-campanulate, 11–21 mm long, 5–10 mm wide at middle in fruit, generally canescent-tomentose and setose with blackish or whitish glandless setae; outer bracts 8–10, lanceolate, acute, the longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner; inner bracts 8–18, lanceolate, acute, pubescent on inner face with appressed shining hairs, becoming carinate dorsally in fruiting heads and spongy-thickened toward the base; receptacle areolate, glabrous; corollas 13–22 mm long; ligule about 3 mm wide; corolla tube about 5 mm long; anther tube (3.5)6 \times 1(1.75) mm dis.; appendages about 0.8 mm long, oblong, obtuse; filaments 0.7 mm longer; style branches 1.8–3.5 mm long, about 0.2 mm wide, yellow; achenes blackish or greenish or (chiefly in forms of subsp. *subacaulis*) brownish or reddish, 7–12 mm long, about 1 mm wide; \pm attenuate to the apex or coarsely beaked, usually paler at the expanded pappus disk and at the finely calloused hollow base, with about 10 low rather indistinct ribs, smooth or finely spiculate; pappus dusky or yellowish-white, 5–13.5 mm long, 4–6-seriate, the setae \pm united at the base and coming away in clumps, unequal, the outermost shortest and finest, the coarsest about 50 μ (5–6 cells) wide at the base, persistent. Flowering May–July; flowers yellow. Chromosomes, $2n = 22!$, 33?, 44!, 55?, 66?, 88?

Montana to S. British Columbia and central Washington, E. Oregon and N.E. California, east to Colorado, Utah, Nevada, and, in one locality, in S. California.

Four subspecies have been recognized, two of which, subsp. *typica* and subsp. *rostrata*, include both diploid and polyploid forms.

Key to the Subspecies of C. modocensis

Setae on the stem and petioles stiff and yellowish, those on the involucre blackish, all straight or slightly curved, not conspicuously crisped (in some forms of subsp. *subacaulis* whitish and crisped, but these have brownish achenes).

Stems low or tall, rather slender and generally branching from $\frac{1}{3}$ of the way up or higher; largest involucre 13–16 mm long in fruit; pappus 5–10 mm long. 118, a. **typica**

Stems low, rather stout, generally branching from near the base; largest involucre 15–21 mm long in fruit; pappus 9–13.5 mm long. 118, b. **subacaulis**

Setae all or nearly all whitish, elongated, and conspicuously curled or crisped; those on the involucre generally very dense; achenes always greenish or blackish.

Stems 1.5–3 dm high; involucre 14–17 mm long; corollas 18–22 mm long; achenes \pm beaked, 7–10 mm long; pappus 7–10 mm long. 118, c. **rostrata**

Stems 0.6–1.3 dm high; involucre 11–13 mm long; corollas 14–16 mm long; achenes merely attenuate, not beaked, 6–7 mm long; pappus 5.5–6.5 mm long. 118, d. **glareosa**

118, a. ***Crepis modocensis typica*** Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 142. 1938. Plants variable in size and habit but always with a well-developed primary axis; basal leaves narrowly elliptic; stems mostly branched near or above the middle; involucre 11–16 mm long, the bracts always setose throughout their length; achenes 7–12 mm long, weakly striate or nearly smooth, varying from greenish-black to deep reddish-brown, longer than the pappus; pappus 5–10 mm long. See fig. 169, a–e, o, o'.

Crepis modocensis Greene, loc. cit., 1895.

C. scopulorum Coville, Contr. U. S. Nat. Herb. 3: 563. 1896.

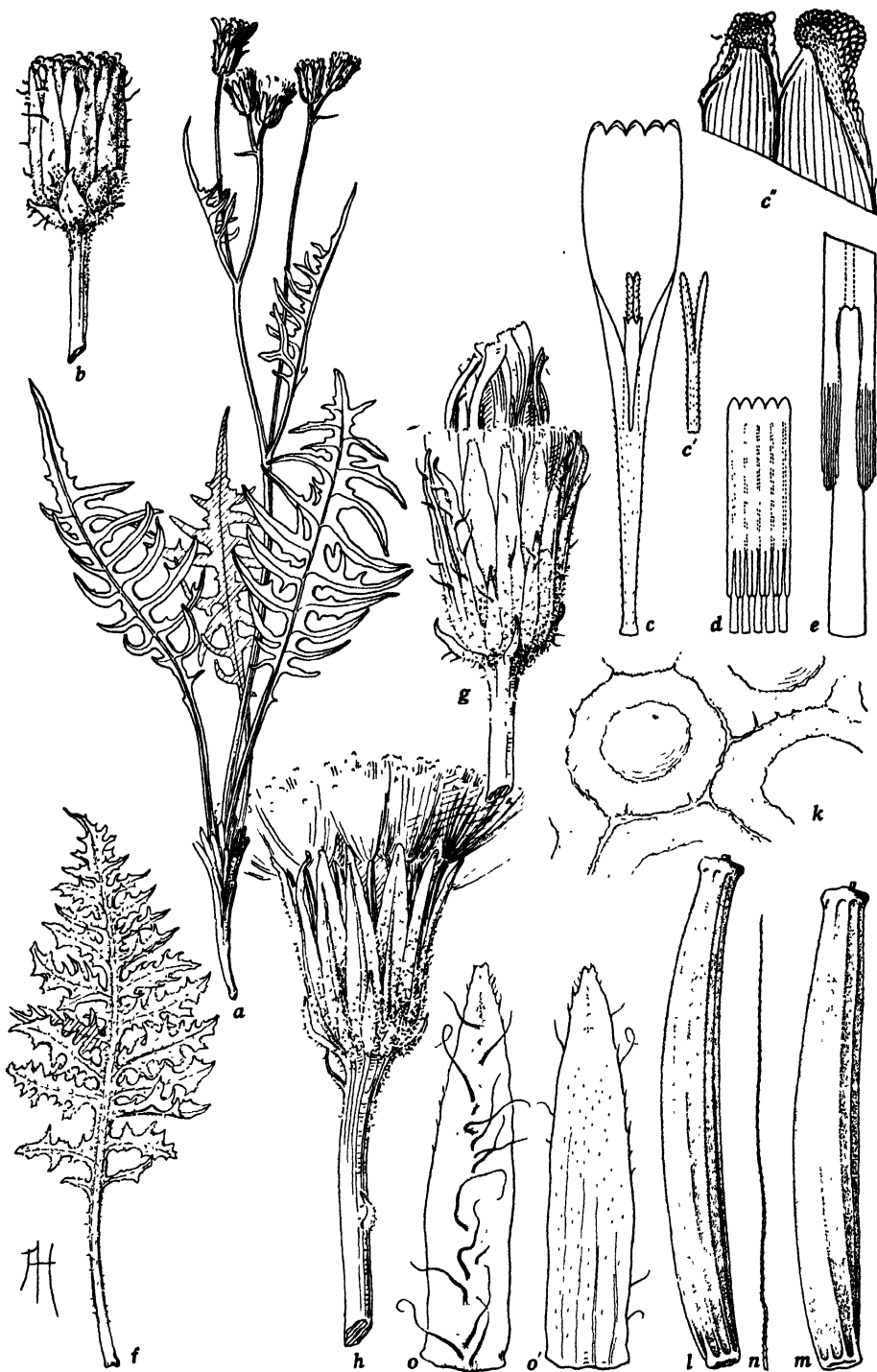


Fig. 169. *Crepis modocensis*, a-e, subsp. *typica* near apm. *pauciflora*, from Baker 148 (UC 91869); f-g, subsp. *subacaulis* apm. *multiflora*, from Smith in 1927 (UC 346584); h, k-n, subsp. *subacaulis* near apm. *grandiceps*, from Babcock and Navashin 121 (UC 346530); o, o', subsp. *typica* apm. *elator*, from Clark 29 (UC 163304): a, plant, $\times \frac{1}{2}$; b, young head, $\times 2$; c, floret lacking ovary, $\times 4$; d, style branches, $\times 4$; e, detail of ligule teeth, $\times 50$; f, detail of appendages, $\times 32$; g, head in anthesis, $\times 2$; h, fruiting head, $\times 2$; i, detail of receptacle, $\times 25$; j-n, 2 achenes and a pappus seta, $\times 8$; o, o', inner involucral bract, outer and inner faces, $\times 4$.

Range of the species, except that it is replaced by subsp. *subacaulis* in the Lake Tahoe reg. and in S. California, and by subspp. *rostrata* and *glareosa* in central Washington.

This subspecies includes a diploid form and several polyploid apomictic forms. The diploid form is a low plant, with slightly tomentulose but densely setose stems and leaves; an inflorescence of 1–4 heads, which are many-bracted and many-flowered; and deep greenish or blackish achenes. Some of the polyploid forms are transitional toward *C. acuminata* and others, toward subsp. *subacaulis* and, therefore, toward *C. occidentalis*. For a key to these forms and citation of specimens under each, see Babcock and Stebbins (*op. cit.*, 144–147). The specimens cited below comprise all of the known collections of the diploid form.

Oregon: Harney Co., Steins Mts., *Cusick* 1988, part (UC). **California:** Modoc Co., Lake City Mt., *Bruce* 2164, part (UC, DS); Modoc Co., west of Cedarville, 1515–1666 m, *Babcock and Stebbins* 1808A (UC); Lassen Co., near Susanville, Diamond Mt., 2200 m, *Stebbins and Jenkins* 2276 (UC).

118, b. ***Crepis modocensis subacaulis*** (Kellogg) Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 148. 1938. Plants mostly 0.6–2 (rarely 2.5–3) dm high; basal leaves somewhat broader than in subsp. *typica*, often bipinnatifid or the lobes conspicuously toothed; stems mostly branching from near the base, bearing 1–5 heads; involucre 13–21 mm high, the bracts usually less setose than in subsp. *typica*, sometimes without any setae; achenes varying from blackish to brownish or reddish, more strongly ribbed than in subsp. *typica*; pappus 9–13.5 mm long, equal to or longer than the achene. See fig. 169, f–n.

Crepis occidentalis var. *subacaulis* Kellogg, Proc. Cal. Acad. 5: 50. 1873.

C. occidentalis var. *nevadensis* Kellogg, loc. cit.

C. subacaulis Coville, Contr. U. S. Nat. Herb. 3: 562. 1896.

S. Oregon in the Warner Mts., and California in the N. Sierra Nevada and San Bernardino Mts.

This subspecies consists of a series of forms which are transitional, chiefly between typical *C. modocensis*, i.e., the diploid form of subsp. *typica*, and *C. occidentalis*; but some of the forms approach *C. monticola*. For a key to these forms and citation of specimens under each, see Babcock and Stebbins (*op. cit.*, 149–152). The specimens cited below include only the type of subsp. *subacaulis* and closely similar plants in which the diploid chromosome number is probably 44.

California: Placer Co., Cisco, *Kellogg and Brannon* in 1870 (G) type collection of *C. occidentalis* var. *subacaulis* Kellogg; Sierra Nevada, Summit, *Kellogg* in 1870, part (G); *ibid.*, *Bolander and Keller* in 1872 (G, CA); Nevada (¶) Co., vicinity of Truckee, 2100–2600 m, *Hitchcock* 388 (US). **Nevada:** Washoe Co., Peavine Mt., *Heller* 9715, part (DS).

118, c. ***Crepis modocensis rostrata*** (Coville) Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 152. 1938. Plants 1.5–3 dm high; stems densely setose with white crisped trichomes or merely tomentulose; basal leaves 10–15 cm long, the blade glabrate or tomentulose, the midrib and usually the petiole setose; inflorescence of 1–6 heads on mostly elongated stout peduncles; heads large, with 18–60 florets; involucre 14–17 mm long; inner bracts covered with long whitish crisped setae; corollas 14–22 mm long; achenes greenish-black to somewhat yellowish, 7–10 mm long, gradually attenuate into a coarse beak 0.5–2.5 mm long, the ribs alternately weaker and stronger; pappus 7–10 mm long, shorter than or equal to the achene. Chromosomes, $2n = 22 \text{ f}, 33 \text{ f}, 44 \text{ f}$. See fig. 170.

Crepis rostrata Coville, Contr. U. S. Nat. Herb. 3: 564. 1896.

C. occidentalis var. *orinita* Gray, Bot. Cal. 1: 435. 1876, with respect to material from Washington.

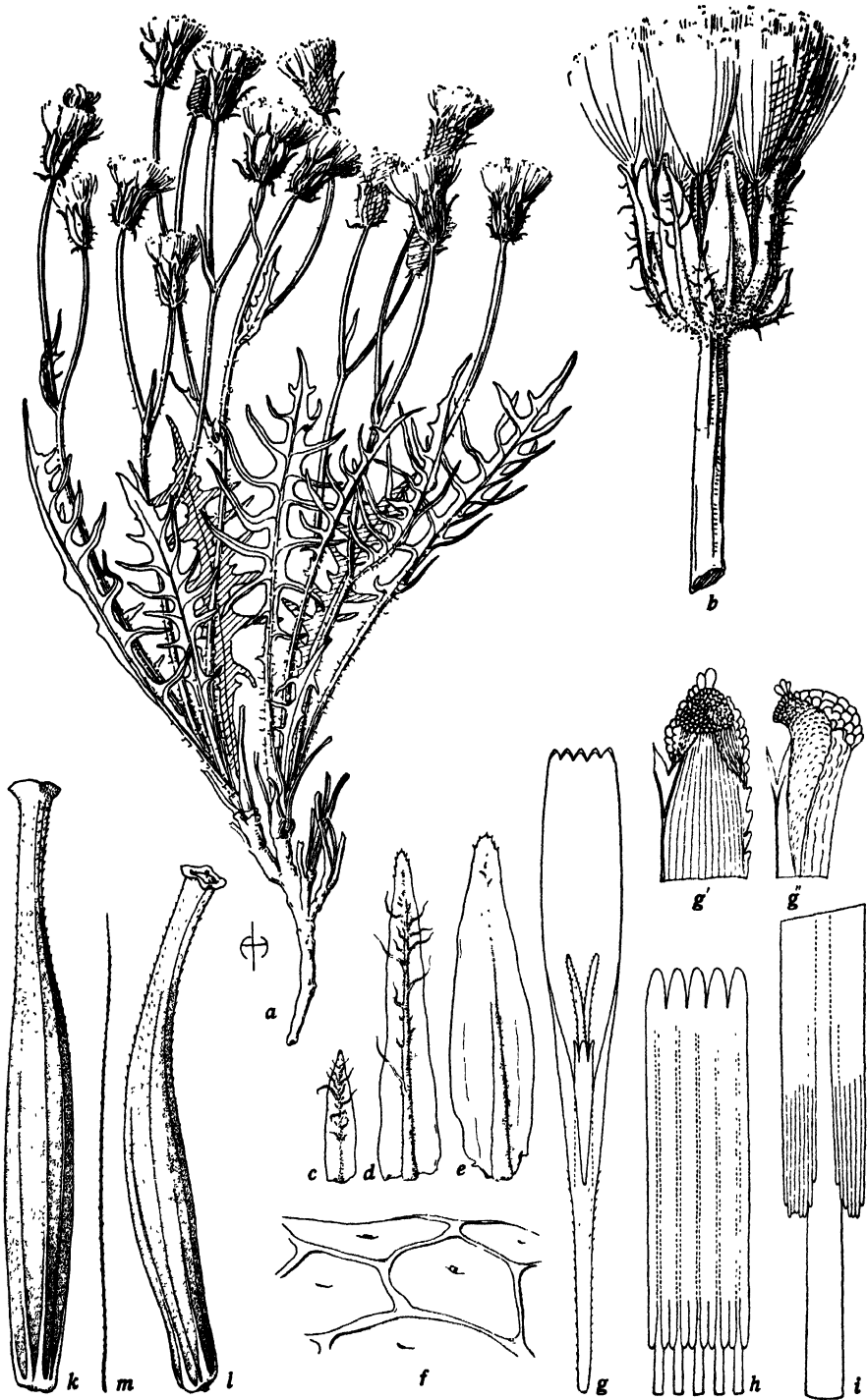


Fig. 170. *Crepis modocensis rostrata*, from isotype (UC 182843): *a*, plant, $\times \frac{1}{2}$; *b*, fruiting head, $\times 2$; *c-e*, outer and 2 inner involucral bracts, outer face, $\times 4$; *f*, detail of receptacle, $\times 25$; *g*, floret lacking ovary, $\times 4$; *g'*, *g''*, details of ligule teeth, $\times 50$; *h*, anther tube, $\times 8$; *i*, detail of appendages, $\times 32$; *k-m*, 2 achenes and a pappus seta, $\times 8$.

Central Washington and S. British Columbia.

Although the range of this subspecies does not overlap with that of subsp. *typica* or subsp. *subacaulis*, the morphological differences are not sufficiently marked or consistent to warrant its recognition as a species, since intergrading forms occur. Evidently both diploid and polyploid forms are included in this subspecies. The latter are mostly stouter and have somewhat larger heads and corollas, and their achenes are often less strongly beaked. They occur most frequently in the same localities as the diploid forms and both have been included in some collections.

Washington: Grant Co., near Crab Creek, 720 m, *Sandberg and Leiber* 225 (UC type, G, Or); Grant Co., Wilson Creek, *Sandberg and Leiber* in 1893 (Minn); Grant Co., near Coulee City, *Thompson 6174* (DS, G, Blake); Kittitas Co., north of Ellensburg, *Thompson 8252* (UC, DS, RM, CA, Blake); Kittitas Co., near Liberty, 1060 m, *Thompson 11548* (CA, WSC, Blake); Yakima Co., upper Naches R., *Grant* in 1930 (UC, Blake); Yakima Co., south of Tieton R., *Warren 1807* (Blake); between the Naches (Spipen) and Wenatchee (N. branch of the Columbia) rivers, *Wilkes Expedition* in 1841 (G, NY); Klickitat Co., Goldendale, *Howell* in 1879 (Or). **British Columbia:** Spence's Bridge, *Thompson R., Fletcher* in 1885 (G).

118, *d. Crepis modocensis glareosa* (Piper) Babc. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 154. 1938. Plants 0.6–1.3 dm high; stems stout, 1–3-headed, canescent-tomentulose, with no or very few setae; basal leaves 4–7 cm long, tomentulose or glabrate, setose along the midrib with long curled whitish trichomes; peduncles stout, about 3 cm long; involucre 11–13 mm long, densely hirsute with whitish curled glandless setae; corollas 14–16 mm long; anther tube about 6 mm long; style branches about 2 mm long; achenes greenish or yellowish, 6–7 mm long, merely attenuate at the apex, striate; pappus 5.5–6.5 mm long.

Crepis glareosa Piper, Bull. Torr. Bot. Club 28: 42. 1901.

Known only from the type collection.

Since the type locality is within the range of subsp. *rostrata*, this plant might be considered to be a dwarf variant of that subspecies. But on account of the conspicuous differences in the achenes and pappus, it is recognized for the present as a subspecies.

Washington: Ellensburg, *Piper 2704* (US 529426 type, G).

Relationship

Crepis modocensis is a very distinct species, of which *C. hokkaidoensis* may have been the 4-paired ancestor. In the latter species the achenes are shaped similarly to those of *C. modocensis rostrata*; but the ribs are more numerous and finer. The involucre in the two species are similar; but in *C. hokkaidoensis* the leaves are less deeply pinnatifid and the root is praemorse. However, the deeply penetrating root and bipinnatifid leaves, characteristic of *C. modocensis*, might have come from a 7-paired ancestral species, such as *C. flexuosa*.

119. *Crepis pleurocarpa* Gray

Proc. Am. Acad. 17: 221. 1882. (Fig. 171.)

Perennial, 1.5–6 (mostly 2–4) dm high, the leaves and stem usually greenish rather than grayish, tomentulose or glabrate, sometimes gland-pubescent; root slender, elongated, woody; caudex swollen, simple or 1-furcate, covered with brown bases of old leaves; caudical leaves 7–28 cm long, 0.5–7 cm wide, elliptic or oblanceolate, acute or acuminate, denticulate or dentate or runcinate-pinnatifid with deltoid lobes or pinnately divided with remote lanceolate acuminate sometimes dentate lobes and with the terminal segment 1–7 cm long, attenuate-acuminate; cauline

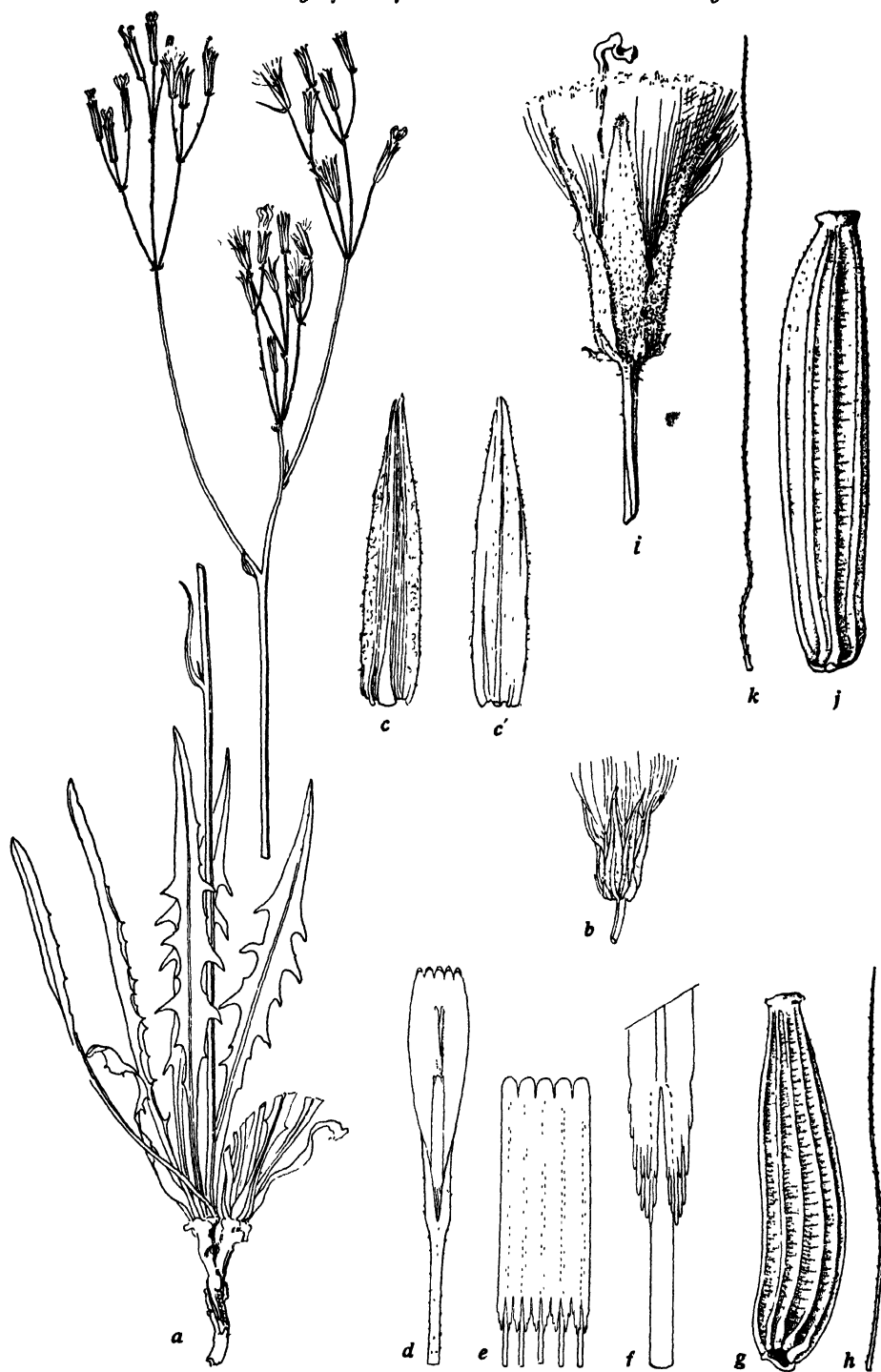


Fig. 171. *Crepis pleurocarpa*, a-h, diploid form, from Stebbins and Jenkins 2471 (UC 581310); i-k, apm. *attenuata*, from Tracy 2794 (UC 164830): a, plant, $\times \frac{1}{2}$; b, fruiting head, $\times 2$; c, c', inner involucre bract, outer and inner faces, $\times 4$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, h, achene and pappus seta, $\times 8$; i, immature head, $\times 2$; j, k, achene and pappus seta, $\times 8$.

leaves few, sessile, gradually reduced; stems 1–2 or rarely 3, slender or stoutish, terete, striate, branched above the middle or remotely few-branched beginning near the base, branches strict or fastigiate, the lower elongated, each branch or the simple stem cymosely branched near the summit, forming small corymbiform clusters of heads; peduncles 1–3 cm long, slender, becoming slightly thickened and sulcate near the head; heads 7–40, mostly 15–30 in the aggregate inflorescence, erect, small, 4–12-flowered; involucre cylindric-campanulate, 8–16 mm long, 3–5 mm wide at middle; outer bracts 5–6 with 1–3 subtending ones, small, the longest 1.5–4 mm long, lanceolate or deltoid, acute; inner bracts mostly 5, in a few forms 6–8, lanceolate, 2–4 mm wide, mostly acute, sometimes strongly attenuate toward the apex, sometimes rounded at the very tip, deep green, or blackish in sic., with conspicuous scarious margins, these densely floccose-tomentulose, the middle part glabrate, becoming dorsally carinate and spongy-thickened at maturity, pubescent on inner face; receptacle areolate, glabrous or shortly ciliate; corollas 15–20 mm long; ligule about 2 mm wide; teeth 0.4 mm long; corolla tube about 5 mm long, shortly pubescent from base to lower part of ligule; anther tube 4.5–6.5 mm long; appendages about 0.6 mm long, lanceolate, acute; filaments about 0.6 mm longer; achenes deep chestnut brown, 5–8 mm long, about 1.5 mm wide, oblong, slightly or sometimes more strongly contracted at the apex, paler at the pappus disk and the strongly calloused hollow base, 10-ribbed, the ribs equally prominent, smooth or finely spiculate; pappus pale yellowish, dusky or white, 6–12 mm long, 4–6 seriate, the setae unequal, 35–85 μ (3–8 cells) wide at the base, the outermost shortest and finest, persistent. Flowering June–Aug.; flowers yellow. Chromosomes, $2n = 22!$, 33?, 44?, 55?, 77?, 88?

Crepis intermedia var. *pleurocarpa* Gray, Syn. Fl. 1(2): 432. 1884.

C. acuminata var. *pleurocarpa* Jepson, Man. Fl. Pl. Calif. 1012. 1925.

N. California, southward in the Coast Ranges to Lake Co. and in the Sierra Nevada to Eldorado Co.; S.W. Oregon and northward to Curry and Douglas counties; central Washington in the Wenatchee Mts.

C. pleurocarpa has been confused with both *C. acuminata* and *C. intermedia*; but it is distinct in its inner involucre bracts with a conspicuous white-tomentose margin and glabrate middle part, also in its broader, more strongly ribbed achenes and longer pappus. There are remarkably few intermediate forms between *C. pleurocarpa* and *C. acuminata*, although both are connected with *C. intermedia* and, through it, with *C. occidentalis*. Furthermore, *C. pleurocarpa* has a geographical range very different from either *C. acuminata* or *C. intermedia*; and in its ecological habitat it differs from all the American species of *Crepis*. Not only does it occur exclusively in the humid climatic belt, but within this area it has been collected only along streams in dense coniferous forests. Although it occurs chiefly on well-drained sites, one colony was found in a moist, boggy spot with species of *Carex*, *Helenium*, and *Rudbeckia*.

In addition to the diploid form, all the known specimens of which are cited below, 11 apomictic forms, including apm. *plumaënsis*, have been described. For a key to these forms and citation of specimens, see Babcock and Stebbins (*op. cit.*, pp. 109–114). The type, collected by Pringle in 1881, is in Gray Herb. The two plants in herb. Boissier should be compared with apm. *humilis*, since this collection, Pringle in 1882, includes this form.

California: Siskiyou Co., near Mt. Shasta, Sulloway Creek, *Smith 474* (G, CA, Clo); Mt. Eddy, 1818 m, *Copeland 3755*, part (G); Sisson's (Mt. Shasta), *Brandege* in 1887, part (UC); Siskiyou Co., T. 41 N., R. 5 W., Parks Creek, below Stewart's Springs, 1125 m, *Stebbins and*

Jenkins 2434 (UC); Trinity Co., along Trinity R., north of Carrville, 910–1060 m, Stebbins and Jenkins 2462, 2463, 2471 (UC) Trinity Co., Scott Mts., Tangle Blue Creek, 1515 m, Howell 12804 (CA).

Relationship

C. pleurocarpa does not have a recognizable affinity with any Old World species. It is essentially endemic in N. California and adjacent Oregon, and its diploid form, like that of *C. monticola*, is narrowly restricted to a geologically and floristically ancient region. Hence, it may well represent a type older than any other small-headed species in this section; and its broader, more strongly ribbed achenes are consistent with this conception.

120. *Crepis acuminata* Nutt.

Trans. Am. Phil. Soc. n.s. 7: 437. 1841. (Fig. 172.)

Perennial, 2–6.5 dm high, with grayish-green foliage; root slender or stout, woody, elongated into a deep taproot; caudex \pm swollen, simple or 1–2-furcate, covered with brown bases of old leaves; caudical leaves 12–40 cm long, 0.5–11 cm wide, the blade elliptic-lanceolate, pinnately lobed with 5–10 pairs of lateral segments, the apical part 3–8 cm long, gradually attenuate, acuminate, the lateral lobes 0.7–3 cm long, 0.2–1.2 cm wide, acuminate, entire or dentate, the blade attenuate into a usually long narrowly winged stout petiole with broader clasping scarious base, the whole leaf densely or sometimes sparsely canescent-tomentose; cauline leaves few, remote, the lower similar to the caudical or sessile, gradually reduced, uppermost linear or bractlike; stems 1–3, erect, stout, striate or sulcate, tomentose at least near the base, branched from near or above the middle, lower branches elongated, branched and sometimes rebranched, the aggregate inflorescence a compound corymbiform cyme with 15–240 or usually 30–100 heads; peduncles 0.2–2 cm long, slender, slightly larger near the head, sulcate, glabrous or tomentulose; heads erect, small, 5–12-flowered; involucre cylindric-campanulate, 9–15 mm long, 2.5–4 mm wide at middle just before completely mature; outer bracts 5–7, lance-deltoid, 1–3 or rarely up to 6 mm long, acute, strongly ciliate on the margin; inner bracts 5–8, yellowish or olive green, 1.5–2.5 mm wide, lanceolate, obtuse, ciliate at the apex, glabrous or tomentulose on outer face, glabrous on inner face, becoming strongly carinate dorsally toward the base and pale spongy-thickened confluent with the base, ultimately reflexed; receptacle areolate, glabrous; corollas 10–18 mm long; ligule 2.2–3.5 mm wide; teeth 0.5 mm long; corolla tube 3.5–5.5 mm long, very shortly pubescent or scabridulous with minute conical 2-celled trichomes, these sometimes sparse, appressed, inconspicuous; anther tube 3–7 mm long; style branches 1.5–3 mm long, yellow; achenes pale yellow or brownish, 5.5–9 (mostly 6.5–8) mm long, 1–1.2 mm wide, \pm attenuate to the apex, narrowed at the callosed hollow base, about 12-ribbed, the ribs rather narrow but fairly strong, often somewhat unequal, finely spiculate toward the apex; pappus dusky white, 5.5–9 mm long, 4-seriate, the setae united at the base and coming away in clumps, unequal, the outermost shortest and finest, the coarsest about 60μ (6–7 cells) wide at the base, persistent. Flowering May–Aug.; flowers yellow. Chromosomes, $2n = 22!$, $33!$, $44!$, $55?$, $88?$

Montana to Washington, southward to N. New Mexico, N. Arizona, central Nevada, and the mountains of S. California.

Two subspecies have been recognized, as follows:

- Involucres with 5–8 inner bracts and 5–10 florets.....120, *a. typica*
 Involucres with strictly 8 inner bracts and 9–12 florets.....120, *b. pluriflora*

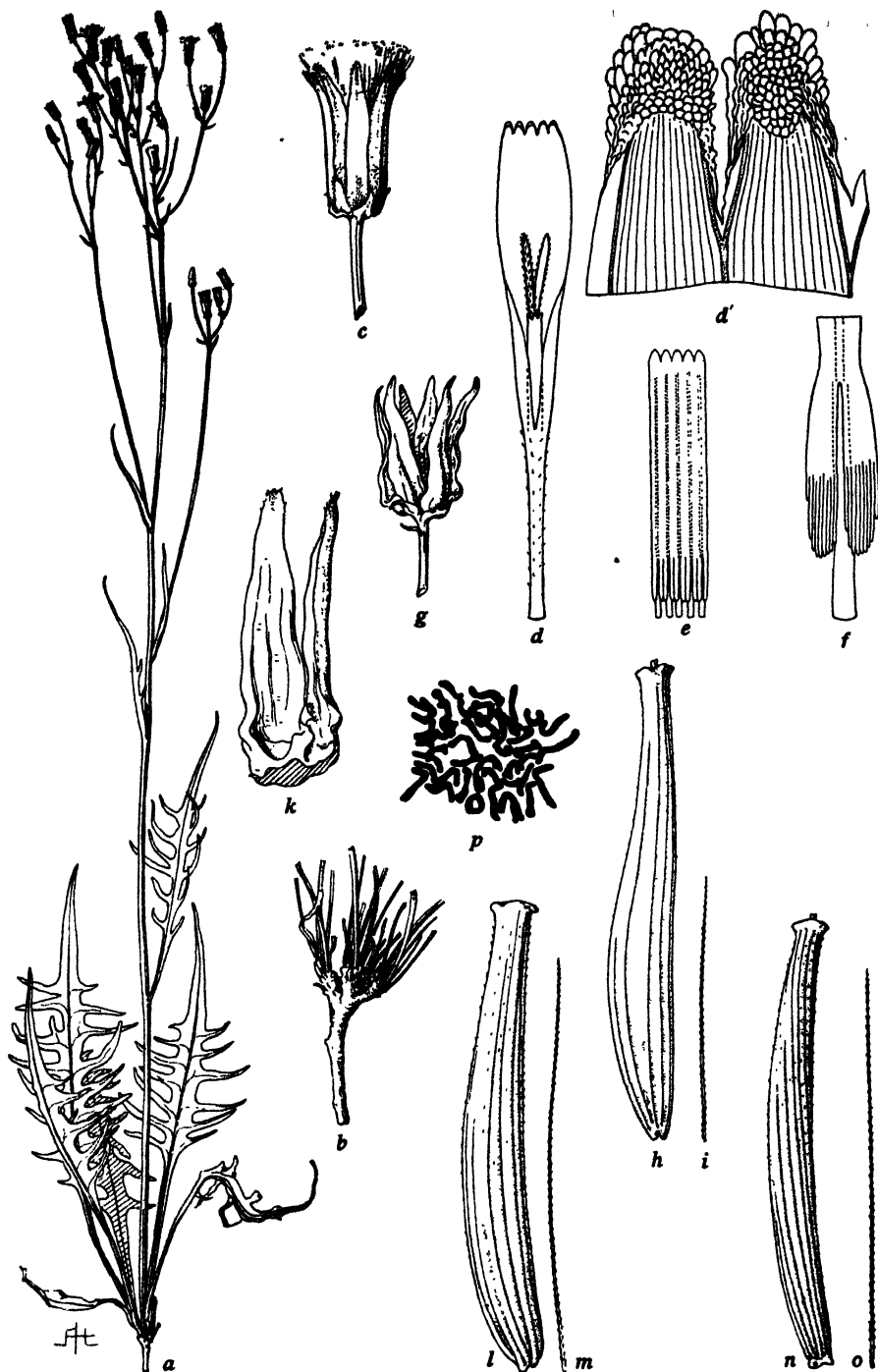


Fig. 172. *Crepis acuminata* typica, a-f, apm. *sierrae*, a, c-f, from Baker 386 (UC 62944); b, from Babcock 148 (UC 346498); g-k, diploid form, from Hall 11510 (UC 216990); l, m, near apm. *longiloba*, from Larkins in 1904 (UC 62949); n, o, apm. *depauperata*, from Davidson 2599 (UC 159914); p, from hort. genet. Calif. 1778 (grown from roots collected by Babcock, near Reno, Nev.): a, plant, $\times \frac{1}{4}$; b, base of old plant, $\times \frac{1}{4}$; c, young flower head, $\times 2$; d, floret lacking ovary, $\times 4$; d', detail of ligule teeth, $\times 50$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, mature head, $\times 2$; h, i, achene and pappus seta, $\times 8$; k, inner bracts showing inner (and part of outer) face and adjacent receptacle, $\times 4$; l-o, achenes and pappus setae, $\times 8$; p, somatic chromosomes of a polyploid form, $2n = 44$ ♀, $\times 1250$.

120, a. *Crepis acuminata typica* Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 170. 1938. Characters of the species, except, at least, that most of the involucre of the inflorescence have only 5–7 inner bracts and 5–10 florets. See fig. 172.

Crepis acuminata Nutt., loc. cit.

C. angustata Rydb., Bull. Torr. Bot. Club 32: 135. 1905 in part.

C. seselifolia Rydb., op. cit., 38: 14. 1911.

Hieraciodes acuminatum O. Kuntze, Gen. 345. 1891.

Range of the species, except in S.W. Colorado and adjacent New Mexico.

This subspecies includes the diploid, sexual form, as well as a large series of polyploid, apomictic derivatives. The diploid is the most widespread of all these forms; and in this respect *C. acuminata* differs from all the other species of this section except *C. runcinata*. The diploid form is consequently more variable than the diploid forms of the other species. Throughout most of its range the diploid is relatively easily recognized by its small involucre, 9–12 mm high, which are usually 5- or rarely 6-flowered. In S.W. Oregon and N.W. California, however, where diploid *C. acuminata* occurs together with the polyploid forms of both it and *C. intermedia*, there is much more variation, and diploid forms exist with as many as 8–12 florets and with involucre up to 15 mm high. These can be distinguished from the polyploid forms only by their smaller stomata and their regular pollen, consisting entirely of 3-pored grains. Most of the polyploid apomicts of *C. acuminata* produce no pollen, and in the few having pollen it is very irregular. Morphologically, these forms intergrade very gradually from those indistinguishable from sexual *C. acuminata* to forms differing almost imperceptibly from small-headed, lightly tomentose extremes of *C. intermedia*. Although some of the forms of this subspecies are very distinct from the diploid form, all attempts to group them in separate subspecies, distinguished by recognizable characters and possessing definite ranges, were unsuccessful. For a taxonomic treatment of 16 apomictic forms of subsp. *typica*, see Babcock and Stebbins (op. cit., pp. 171–178). Only sufficient specimens of the diploid form are cited below to indicate its range.

Without definite locality: plains of the Platte, *Nuttall* (G, type of *C. acuminata*; PA, Po). **Montana:** Madison Co., near Pony, Old Hollowtop, 2720 m, *Rydberg and Bessey 5302* (UC, Minn); Gallatin Co., Spanish basin, 1800 m, *Rydberg and Bessey 5301* (G, RM). **Wyoming:** Bighorn Co., head of middle fork of Powder R., *Gooding 323* (UC, DS, Po, RM, Clo); Yellowstone National Park, near Camp Roosevelt, *Babcock 116* (UC); Teton Mts., Coal Gulch, 2270 m, *Hall 11439* (UC). **Colorado:** Larimer Co., mountains, *Osterhout* in 1894 (Minn); Ute Pass, near Manitou, *Letterman* in 1884 (G). **Idaho:** Lemhi Co., Lemhi Range, E. slope, 2575 m, *Hall 11510* (UC); Lincoln Co., Shoshone, *Nelson and MacBride 1176* (UC, RM, Minn). **Utah:** Cache Co., Wellsville Mts., Pine Canyon, *Maguire 3169* (RM). **Oregon:** Union Co., near Kamela, about 1035 m, *Keck and Clausen 3614* (UC); Deschutes Co., Redmond, *Whited 1916* (DS); Lake Co., Warner Mts., Drake Peak, *Applegate 1936* (DS); Klamath Co., Keno, *Peck 9366* (DS); Grant Co., north of Seneca, *Thompson 11949* (CA). **Nevada:** Humboldt Co., Pine Forest Mts., 1500 m, *Taylor and Richardson 13* (UC). **California:** Modoc Co., lava beds, *Baker* in 1893 (UC, Minn, RM); Siskiyou Co., Mt. Shasta, N. side, near Sheep Rock, 1500 m, *Babcock and Stebbins 1964–1972*, *Stebbins and Jenkins 2432* (UC); Shasta Co., near Fall River Mills, Saddle Mt., 1480 m, *Stebbins and Jenkins 2390* (UC); Lassen Co., south of Ravendale, Secret Valley, 1363 m, *Babcock and Stebbins 1776* (UC).

120, b. *Crepis acuminata pluriflora* Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 178. 1938. Differs from subsp. *typica* in its larger involucre, which have consistently 8 inner bracts and 9–12 florets. The bracts, however, are glabrous or nearly so. The anthers are reduced and without pollen; and the style branches are longer than those of diploid *C. acuminata*, but not longer than those of some polyploid forms of subsp. *typica*. The achenes are rather strongly ribbed, but not more so than in some forms of subsp. *typica*.

W. and S.W. Colorado to N. New Mexico, where it is the only form of *C. acuminata* known, and westward to central Utah.

Although all the available specimens of this subspecies had no pollen in their anthers, and hence are nearly or completely apomictic, yet a number of different apomicts apparently exist. Owing to lack of sufficient material, these could not be adequately characterized. This subspecies might well be placed in *C. intermedia*; but, since its glabrous involucre is so characteristic of *C. acuminata*, it is retained in the latter species. The chromosome numbers are probably $2n = 33$ and 44 . The following specimens were seen:

Colorado: Delta Co., Cedar Edge, 2120 m, *Baker 245* (UC 91870 type; Po, Minn, but some specimens of this collection are *C. intermedia*); Routt Co., Williams Fork, *Sturgis* in 1903 (G); Montrose Co., above Cimarron, 2575 m, *Baker 386* (UC, DS, Po, RM, Minn); Grand Co., Sulphur Springs, *Osterhout 3314* (Minn); Montezuma Co., Mancos, *Baker, Earle, and Tracy 66*, part (UC, Clo); Mesa Verde National Park, entrance, 2120 m, *Goodman and Hitchcock 1358* (UC, DS). **New Mexico:** without locality, *Palmer* in 1869 (US). **Utah:** Juab Co., Mt. Nebo, *Rydberg and Carlton 7702* (RM).

Relationship

C. acuminata exhibits considerable resemblance to *C. flexuosa* of Central Asia in its ramose inflorescence, in its glabrous involucre with small outer bracts, and in the shape and color of its achenes. These resemblances are sufficient to suggest that *C. flexuosa*, or some similar 7-paired Asiatic species, was one of the parents of the original 22-chromosome sexual form.

121. *Crepis atribarba* Heller

Bull. Torr. Bot. Club 26: 314. 1899. (Pl. 13; figs. 173, 174.)

Perennial, 1.5–6 dm high, with mostly slender glabrous or tomentulose stems and leaves; root slender, woody, with a long taproot; caudex swollen, simple or 1-furcate, 1–2-stemmed, covered with brown bases of old leaves; caudical leaves 10–35 cm long, 0.5–6 cm wide, lanceolate to linear, pinnately or bipinnately lobed or parted to the narrow rachis, or rarely almost entire, the apical part elongated, gradually attenuate, acuminate, the lateral segments remote, linear or lanceolate, acuminate, often falcate-salient, the blade narrowed into the terete usually long petiole with broader clasping base; cauline leaves few, remote, similar to the caudical or sessile, upper ones linear or bractlike; stem erect, slender, or in some apomictic forms stout, terete, striate, branched usually from above the middle or higher, the branches strict, slender, dichotomously rebranched, forming a compound or simple corymbiform cyme with 3–30 or 40 heads; peduncles 1–4 cm long, slender, slightly thickened and sulcate near the head; heads erect, rather small, 6–35-flowered; involucre cylindric campanulate, 8–14 mm long, 3–5 mm wide at middle just before full maturity, canescent-tomentose, glabrate or rarely glabrous, with or without black glandless setae on the inner and sometimes the outer bracts; outer bracts 5–10, lance-deltoid, acute, the longest $\frac{1}{4}$ – $\frac{1}{3}$ as long as the inner; inner bracts 5–13, lanceolate, acute or obtuse, ciliate at the apex, yellowish margined, glabrous or appressed-pubescent on inner face, becoming carinate dorsally and pale spongy-thickened toward the base, ultimately spreading or reflexed; receptacle areolate, with naked, fimbriate, or ciliate interspaces; corolla 10–18 mm long; ligule 1.75–2.5 mm wide; teeth 0.2–0.5 mm long; corolla tube 4–7 mm long, sparsely and very shortly pubescent or scabridulous with conical trichomes; anther tube $(3.5)6 \times 1.5$ (1.75) mm dis., in some forms abortive; style branches 1.5–3 mm long, yellow; achenes 3–10 mm long, 0.8–1.3 mm wide, of various shades of green or rarely brown, \pm attenuate toward the apex, narrowed at the calloused base, 12–15-ribbed, the ribs mostly rather prominent, rounded, smooth or finely spiculate; pappus white

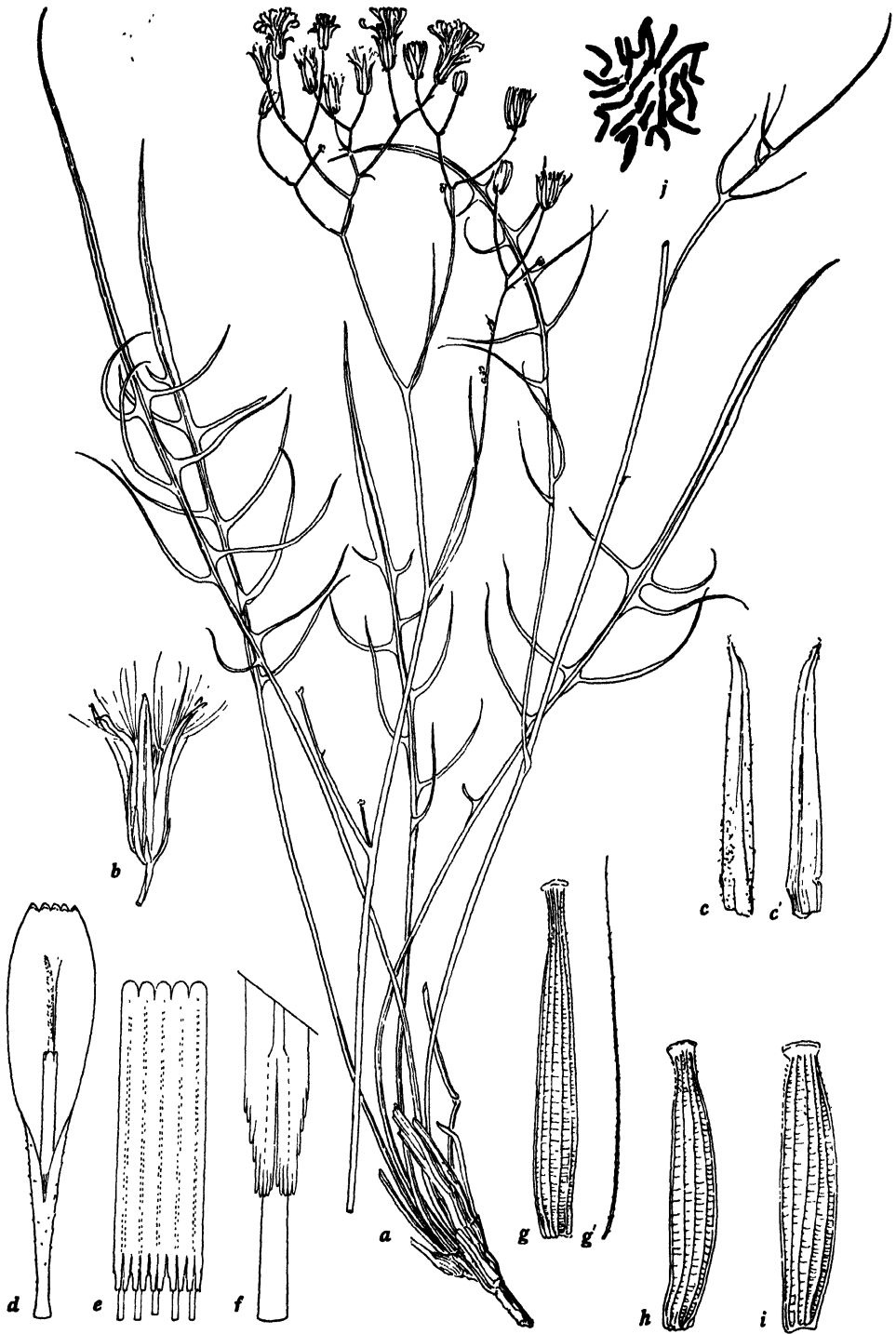


Fig. 173. *Crepis atribarba originalis*, diploid form, from Wheeler in 1928 (UC 346445, 346452): a, plant, $\times \frac{1}{4}$; b, fruiting head, $\times 2$; c, σ , inner involucre bract, outer and inner faces, $\times 4$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, immature achene and a pappus seta, $\times 8$; h, i, achenes from 2 closely similar plants of same collection, $\times 8$; j, somatic chromosomes, $2n = 22$.

or whitish, 5–9 mm long, 2–4-seriate, the setae nearly equal and rather fine, or very unequal with the finest ones on the outer margin, persistent. Flowering June–July; flowers yellow. Chromosomes, $2n = 22!$, $33?$, $44?$, $55!$, $88!$

Montana to British Columbia and southward to Colorado, Utah, Nevada, and central Oregon.

Unfortunately, the oldest name for this species, *C. gracilis* (D. C. Eaton) Rydb., had to be given up because of the priority rule (see below for synonymy). For the same reason the name adopted by Babcock and Stebbins (504: 159), but immediately corrected by them, i.e., *C. exilis* Osterhout, could not be used. The nomenclatural type of *C. atribarba* is one of a few polyploid, apomictic forms comprising subsp. *typica*. This subspecies is distinguished from the rest of the inclusive species, i.e., from subsp. *originalis*, by the somewhat shorter, stouter stems, the fewer, larger heads, and the broader involucre, with black setae on the inner bracts. *C. modocensis* is believed to be involved in the ancestry of each of these apomicts in subsp. *typica*. They are widespread throughout the Rocky Mountain region, extending westward to E. Washington and N.E. Oregon, where they occur chiefly in the mountains. In the latter regions there is a large series of forms connecting typical *C. atribarba* with the polyploid forms of subsp. *originalis* and, through them, with the diploid form. These polyploid forms of subsp. *originalis* are spread throughout the range of the species and, like the much more restricted diploid form, they occur at lower altitudes. They are taller and have a larger inflorescence with smaller heads, and their involucral bracts are nearly or quite devoid of setae. Since these two series possess different geographic ranges and occupy different habitats, they constitute different subspecies, which are differentiated as follows:

- Stems 3–7 (mostly 3.5–5) dm high; heads 10–30 or more in an inflorescence; involucral bracts without setae, or the setae few and confined to the apical part.....121, *a. originalis*
 Stems 1.5–3.5 dm high; heads 3–18 in an inflorescence; involucral bracts bearing black glandless setae throughout their length.....121, *b. typica*

121, *a. Crepis atribarba originalis* Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 162. 1938. Stems 3–7 dm high; leaves mostly with linear falcate salient entire lobes, usually glabrate; inflorescence strictly dichotomous or with a well-defined primary axis, bearing 10–40 heads; involucre variable but mostly narrower than in subsp. *typica*, the inner bracts without setae or bearing a few glandless setae near the apex; outer bracts mostly short, the longest about $\frac{1}{4}$ the length of the inner; florets, achenes, and pappus more variable than in subsp. *typica*, but not consistently different. See pl. 13 and fig. 173.

Crepis occidentalis var. *gracilis* D. C. Eaton, Rep. U. S. Geol. Expl. 40th Par. 5: 203. 1871, in part.
C. acuminata var. *gracilis* Torr., ex Eaton, loc. cit.

C. intermedia var. *gracilis* Gray, Syn. Fl. 1(2): 432. 1884, in part.

C. gracilis Rydb., Mem. N. Y. Bot. Gard. 1: 461. 1900, non Hook. f. et Thoms. ex C. B. Clarke, Comp. Ind. 254. 1876.

C. angustata Rydb., Bull. Torr. Bot. Club 32: 135. 1905, in part.

C. exilis subsp. *originalis* Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 162. 1938.

Almost throughout the range of the species, but rare in the Rocky Mountains, and not occurring at higher altitudes.

This subspecies includes what is considered as the original form of this species, i.e., the diploid, sexual form. For a key to the series of forms comprising this subspecies, and for descriptions and citation of specimens of the *formae apomicticae*, see Babcock and Stebbins (504: 162–167). Only specimens of the diploid form are cited below.

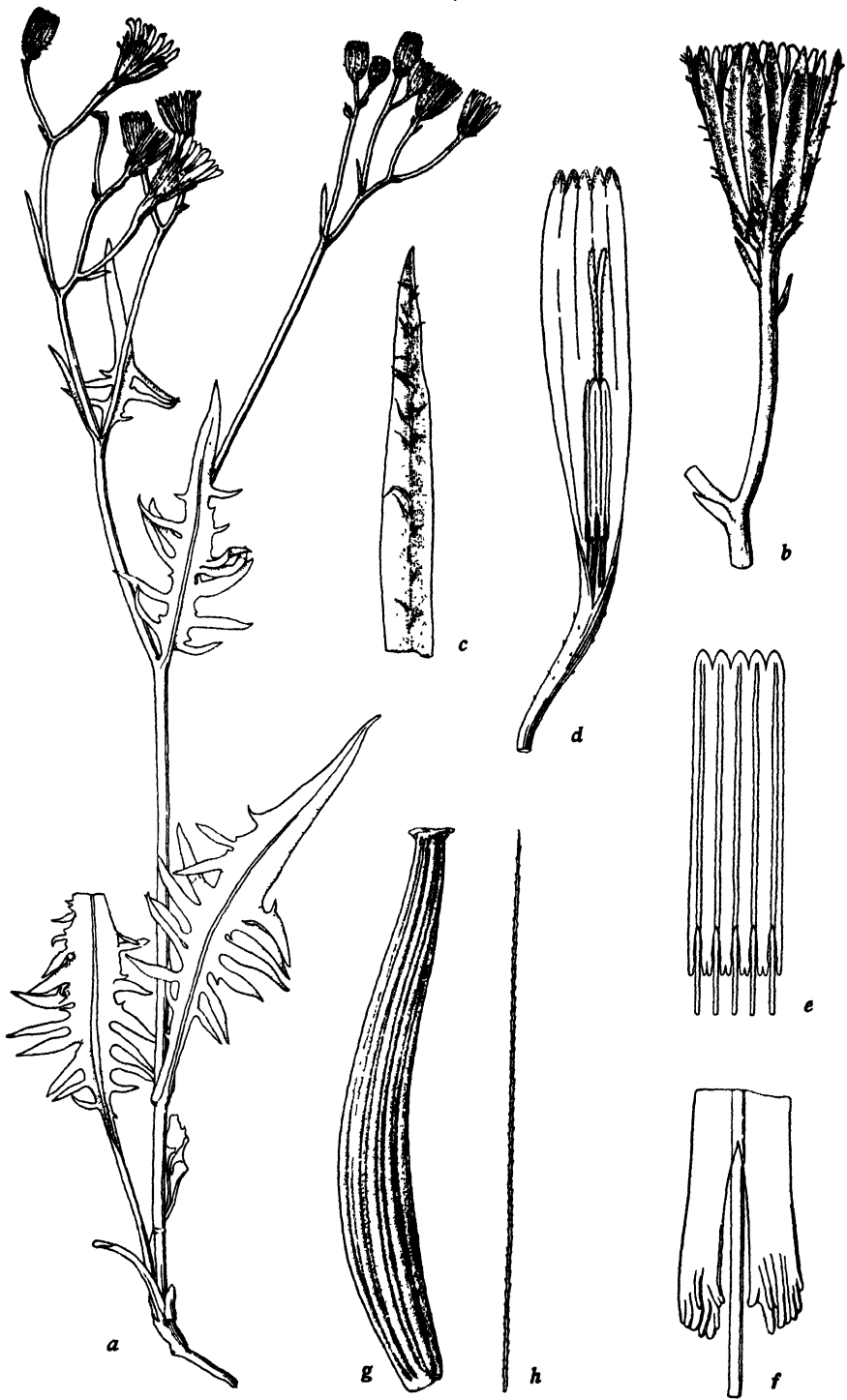


Fig. 174. *Crepis atribarba typica*, apm. *Helleri*; *a-f*, from *Heller 3302* (UC 91876); *g, h*, from *Bates in 1896* (G): *a*, plant, $\times \frac{1}{2}$; *b*, head and peduncle, $\times 2$; *c*, inner involucre bract, from head in anthesis, outer face, $\times 4$; *d*, floret lacking ovary, $\times 4$; *e*, anther tube, $\times 8$; *f*, detail of appendages, $\times 32$; *g, h*, achene and pappus seta, $\times 8$.

British Columbia: near Similkameen R., near Hedley, about 525 m, *Wheeler* in 1928 (UC 346445, type of subsp. *originalis*); Deer Park, Lower Arrow Lake, *Macoun* in 1890 (US); Cascade, near international boundary, *Macoun* 65028 (G, NY, DS). **Washington:** Grant ("Douglas") Co., junction of Crab and Wilson creeks, 475 m, *Sandberg and Leiber* 256, part (UC); Chelan Co., north of Blewett, 500 m, *Keck and Clauson* 3554 (UC); Garfield Co., *Darlington* in 1913 (WSC); Okanogan Co., shore of Okwak Lake, *Fiker* 1258, 1259 (WSC); Franklin Co., north of Kahlotus, *Constance and McMurray* 1159 (WSC); Whitman Co., east of Winona, *Eastwood and St. John* 13217 (WSC); Grant Co., Hartline, 580 m, *Eggleston* 12869 (US); Chelan Co., Chelan, *Jones* in 1911 (Po).

The Eggleston specimen, cited above, is an anomalous form with small heads and exceptionally short achenes, 3–4.5 mm long (see pl. 13, *a*). But this form is not known to have a definite geographic distribution; and it is approached in size of the involucre and achenes by three other specimens previously referred to it as well as by the type collection of the subspecies. Hence, its treatment as a taxonomic segregate does not seem advisable at present.

121, *b. Crepis atribarba typica* Babc. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 167. 1938. Stems 1.5–3.5 dm high, stouter than in the preceding subspecies; heads 3–18, mostly 5–10 in an inflorescence; involucre broader and with more florets; outer bracts longer, the longest about $\frac{1}{3}$ as long as the inner; inner bracts bearing black setae, usually throughout their length. See fig. 174.

Crepis atribarba Heller, *loc. cit.*

C. occidentalis var. *gracilis* Gray, *loc. cit.*, *C. gracilis* Rydb., *loc. cit.*, and *C. exilis* Osterhout, *Muhlenbergia* 1: 142. 1906, all three in part.

C. exilis subsp. *typica* Babc. et Stebbins, Carnegie Inst. Wash. Pub. No. 504: 167. 1938.

British Columbia to Alberta, south to the Blue Mts. of Oregon, and in the Rocky Mts. to Colorado, at higher elevations than subsp. *originalis*.

For a key to the apomictic forms which have been recognized, their descriptions, and citation of specimens, see Babcock and Stebbins (*op. cit.*, pp. 167–169). Only specimens of apm. *Helleri* are cited below.

Idaho: Nez Perces Co., Lake Waha, *Heller* 3302 (UC, US, Minn, type collection of *C. atribarba*). **Washington:** Asotin Co., Blue Mts., *Jones* 979 (Wn).

Relationship

C. atribarba exhibits sufficient resemblance to *C. flexuosa* of Central Asia in its dichotomously branched inflorescence, its type of involucre, and in some forms the small, rather finely ribbed achenes to suggest that the latter species may have been the 7-paired ancestor of *C. atribarba*. No other Asiatic species has been suggested as possibly representing the 4-paired ancestor. It was noted, however, by Babcock and Stebbins (*op. cit.*, p. 31) that in habit *C. atribarba* resembles *Youngia tenuifolia* (Willd.) Babc. et Stebbins. There is also strong resemblance between the two in their leaves. But the diploid form of *Y. tenuifolia* presumably has 5 pairs of chromosomes (cf. B. and S. 484: 47). It is of some significance in this connection that *Y. tenuifolia* partly bridges the gap between *Youngia* and *Crepis* (see Part I, p. 158); and it may have once had a 7-paired relative in *Crepis* which could have been an ancestor of *C. atribarba*.

122. *Crepis intermedia* Gray

Syn. Fl. 1(2): 432. 1884. (Fig. 175.)

Perennial, 3–7 dm high (1.5–3 dm in one dwarf form), with densely or sparsely canescent-tomentose foliage; root stout or slender, woody, elongated into the deeply penetrating taproot; caudex swollen, simple or 1-furcate, covered with brown bases of old leaves; caudical leaves 15–40 cm long, 2–9 cm wide, elliptic-lanceolate, pinnatifid, the apical part long-attenuate, acuminate, the lateral lobes remote or close,

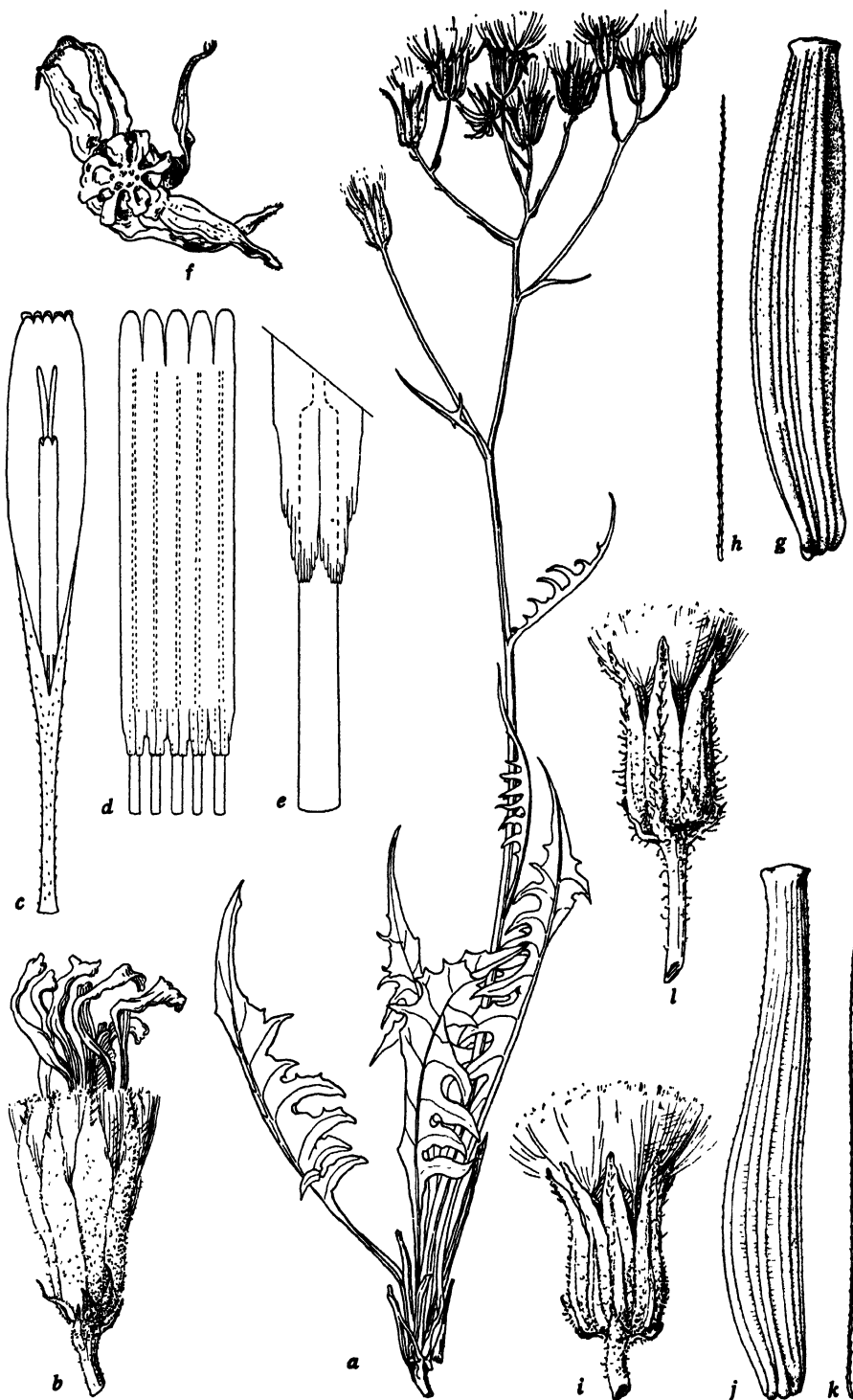


Fig. 175. *Crepis intermedia*, a-h, apm. *arizonica*, from Babcock and Goddard 534 (UC 346593); i-k, near apm. *grandis*, from Babcock 124 (UC 346531); l, near apm. *glandulosa*, from Babcock 127 (UC 346522): a, plant, $\times \frac{1}{2}$; b, flower head, $\times 2$; c, floret lacking ovary, $\times 4$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, old head showing receptacle, $\times 2$; g, h, achene and pappus seta, $\times 8$; i, head, $\times 2$; j, k, achene and pappus seta, $\times 8$; l, head, $\times 2$.

lanceolate, acute or acuminate, entire or dentate, attenuate into a usually long narrowly winged or terete petiole with broader clasping scarious base; cauline leaves few, remote, the lower similar to the caudical or sessile, gradually reduced, uppermost linear or bractlike; stems 1–2, stoutish or stout, erect, terete, striate or sulcate, branched from above or below the middle, lower branches elongated, rebranched near the summit, the aggregate inflorescence a compound corymbiform cyme of 10–60 heads; peduncles 0.5–5 cm long, rather slender, slightly enlarged and sulcate near the head, tomentose; heads erect, medium, 7–12-flowered or rarely 16-flowered; involucre cylindric-campanulate, 10–16 mm long, 4–5 mm wide at middle just before fully mature, canescent-tomentose, glabrate or glabrous, occasionally gland-pubescent or with a few black or green glandless setae near the apex of the inner bracts; outer bracts 6–8, small, lance-deltoid, the longest $\frac{1}{5}$ – $\frac{1}{3}$ as long as the inner; inner bracts 7–8 (rarely 10–12), lanceolate, obtuse, pubescent on inner face, becoming carinate dorsally and pale spongy-thickened toward the base, ultimately spreading; receptacle areolate, glabrous or sparsely ciliate; corollas 14–30 mm long; corolla tube about $\frac{1}{3}$ of the whole corolla length, shortly pubescent or scabridulous; anther tube when well developed 5–8 mm long, or in some forms only 3–4 mm long, abortive, devoid of pollen; style branches 1.75–3.5 mm long, about 0.2 mm wide, yellow; achenes yellowish, buff, or brown, 5.5–9 mm long, 1–2 mm wide, \pm attenuate to the apex, narrowed at the calloused hollow base, 10–12-ribbed, the ribs narrow to rather wide, rounded, smooth or finely spiculate; pappus dusky or yellowish-white, 7–10 mm long, 4–6-seriate, the setae unequal, the outermost shorter and finer, the coarsest up to 80μ wide at base, united at the base and coming away in clumps, persistent. Flowering June–July; flowers yellow. Chromosomes, $2n = 33 ?$, $44 ?$, $55 !$, $88 ?$

Hieraciodes intermedium O. Kuntze, Gen. 345. 1891.

Crepis acuminata var. *intermedia* Jepson, Man. Fl. Pl. Calif. 1012. 1925.

N. California, mostly in the Sierra Nevada, S. central and N.E. Oregon, central and S.E. Washington, S. Alberta, S.W. Wyoming, W. Colorado, Utah, S. Nevada, N. Arizona, and New Mexico. Common in the W. part of its range, infrequent and local eastward.

With the original description of *C. intermedia*, Gray did not cite any specimens; hence there is no type specimen for the species. Most of the specimens in the Gray Herbarium, which were identified by Gray as *C. intermedia*, are more or less fragmentary; but one of the best preserved, which shows both florets and achenes like those described by him, is a collection of Bolander from Yosemite Valley (no. 4930). For practical purposes this may be considered as the type of *C. intermedia*. It is very much like the form recognized by Babcock and Stebbins (*op. cit.*, p. 182) as apm. *Grayi*. For a key to 14 apomictic forms, their descriptions and citation of specimens, see Babcock and Stebbins (*op. cit.*, 181–187). Only specimens of apm. *Grayi* and the Bolander specimen just mentioned are cited below.

California: Fresno Co., Collins Meadow, 2120 m, *Hall and Chandler 540* (UC, DS, Minn); Mariposa Co., Buck Camp, *Congdon* in 1895 (UC, DS, G); Eldorado Co., Sunnyside, *Eastwood 57* (CA); Placer Co. (?), Summit, Sierra Nevada, 2500 m, *Jones 12253* (Po); Sierra Co., west of Loyalton, 1600 m, *Babcock and Stebbins 1711* (UC). **Nevada:** Washoe Co., Verdi, 1550 m, *Stebbins and Jenkins 2173* (UC). The following is close to apm. *Grayi* and is accepted as the type of *C. intermedia*: California: Yosemite Valley, *Bolander 4930* (G).

Relationship

This is an agamospecies, i.e., a group of polyploid apomicts which combine the characters of *C. occidentalis* with those of either *C. acuminata* or *C. pleurocarpa*, or of all three of these species; and some forms possess characteristics of *C. modocen-*

sis and *C. atribarba*. In most forms the habit resembles that of *C. acuminata*. For this reason and because the two species are connected by a continuous series of intergrades, Jepson's merging of *C. intermedia* with *C. acuminata* was to some extent justified. There is, however, an equally gradual transition from *C. intermedia* to *C. occidentalis* subsp. *pumila*, and, so, to typical *C. occidentalis*. Hence, the only logical treatment, based on the existence of intergrading forms, would be to include the whole group under a single species. But this would necessitate the merging of two extremely different entities, *C. acuminata* and *C. occidentalis*, each with its diploid, sexual form. Therefore, viewing this matter from the standpoint that taxonomic units should not only represent as nearly as possible the true state of affairs in nature, but should also be practical, the best procedure is to continue to recognize *C. intermedia* as a species.

123. *Crepis barbiger* Leiberg ex Coville

Contr. U. S. Nat. Herb. 3: 565. 1896. (Fig. 176.)

Perennial, 2–8 dm high, the involucre and often the peduncles and branches beset with long stout glandless yellow or greenish setae; root rather slender, woody, elongated into a deeply penetrating taproot; caudex \pm swollen, simple or 1–2-furcate, each division 1–2-stemmed; caudical leaves erect, up to 40 cm long, 7 cm wide, elliptic-lanceolate, apical part \pm elongated, acute or acuminate, pinnately or bipinnately toothed or (sometimes deeply) parted, lateral segments lanceolate, often falcate and \pm salient, acuminate or acute, the blade tapering into a long stout narrowly winged petiole, with broader clasping scarious base, sparsely canescent-tomentulose or glabrate; cauline leaves similar or sessile, gradually reduced, upper linear or bractlike; stem stout, terete, striate or sulcate, branched above or below the middle, branches elongated, strict, bearing a few short secondary branches near the summit, the secondary and ultimate branches mostly pedunculate, arcuate, the aggregate inflorescence rather congested, cymose-corymbiform; heads few or numerous, erect, medium to large, 8–25-flowered; involucre cylindric, 9–17 mm long, 4–7 mm wide at middle just before beginning to spread open, \pm setose and canescent- or fuscous-tomentose; outer bracts 5–7, lanceolate, acute, 2–5 mm long; inner bracts 7–10, lanceolate, acute or obtuse, usually more densely setose toward the apex, pubescent on inner face, becoming strongly carinate dorsally, carina brown, spongy-thickened at the base, ultimately spreading or reflexed; receptacle areolate-fimbriate, areoles glabrous, fimbriae low, densely ciliate with short pointed yellow trichomes; corolla about 18 mm long; ligule about 3 mm wide; teeth 0.3 mm long; corolla tube about 7 mm long, shortly pubescent or scabridulous with small pointed yellow trichomes; anther tube (5) 6×1.5 mm dis.; appendages 0.75 mm long, obtuse; style branches 1.5–2.3 mm long, yellow; achenes olive green or yellowish, 6–10 mm long, 1–1.5 mm wide, oblong or gradually attenuate to the apex, slightly narrowed at the yellow calloused base, 10–12-ribbed, ribs strong, rounded, finely spiculate toward the apex; pappus whitish or yellowish-white, 6–9 mm long, varying from 2-seriate, the setae nearly equally fine and free at the base, to 3–4-seriate, the setae united at the base, unequal, the coarsest up to 65μ wide at the base, persistent. Flowering June–July; flowers yellow. Chromosomes, $2n = 44!$, $55?$, $88!$

N.W. Idaho, throughout E. Washington to the Cascade Mts., and E. Oregon as far south as Harney Co.

Washington: Douglas Co. near Alkali Lake, 400 m, *Sandberg and Leiberg 313* (US 413938 type, G, UC 167535, CA); Grant Co., Wilson Creek, 600–900 m, *Sandberg and Leiberg* in 1893 (Minn); Kittitas Co., between Cle Elum and Easton, *Thompson 6689* (US, DS); west of Spokane, *Babcock and Collins 61* (UC); S. fork of Ahtanum Creek, *Nelson 1535* (RM).

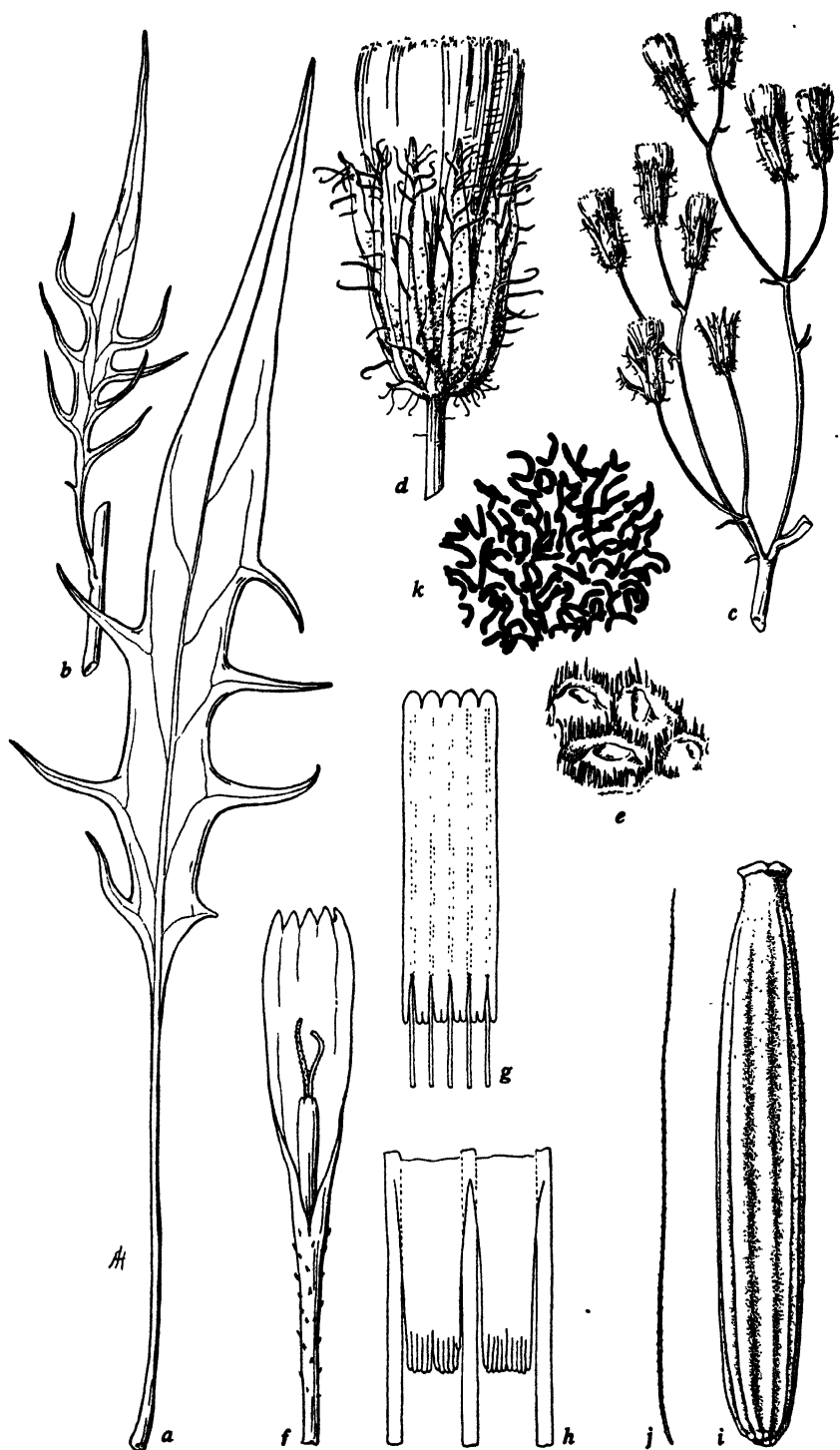


Fig. 176. *Crepis barbiger*, a, b, and d, from isotype (G); c, i, j, from isotype (UC 167535); e-h, from *Suksdorf 378* (G); k, from hort. genet. Calif. 1842 (roots collected in central Washington, *Babcock and Collins 50A*): a, b, caudical and cauline leaves, $\times \frac{1}{2}$; c, part of inflorescence, $\times \frac{1}{2}$; d, head, $\times 2$; e, detail of receptacle, $\times 25$; f, floret lacking ovary, $\times 4$; g, anther tube, $\times 8$; h, detail of appendages, $\times 32$; i, j, achene and pappus seta, $\times 8$; k, somatic chromosomes, $2n =$ about 88, $\times 1250$.

Relationship

Crepis barbiger is an agamospecies, consisting of a series of apomicts which combine characteristics of *C. atribarba*, *C. acuminata*, and *C. modocensis* subsp. *rostrata* or subsp. *glareosa*. Although restricted in range, it is very abundant in the regions in which it does occur, and it is correspondingly variable. The distribution of the various forms, however, agrees well with the supposition that they are derived from intercrossing of the three species mentioned. One form, apm. *dentata*, which approaches most nearly to *C. atribarba*, is within the range of the diploid form of that species. Two other forms, apm. *setosissima* and apm. *laticeps*, which are nearest to *C. modocensis rostrata*, are within the range of that local subspecies. Apm. *breviloba* and apm. *pauciflora*, which occur within the range of diploid *C. acuminata*, approach most nearly that species. For a key to 8 apomicts, their descriptions, and citation of specimens, see Babcock and Stebbins (*op. cit.*, pp. 155–159). Only one form, apm. *Leibergii*, which is the type of the species, and some closely similar specimens, are cited above.

124. *Crepis runcinata* Torr. et Gray

Fl. N. Am. 2: 487. 1843. (Figs. 177–183.)

Perennial, 1–8 (usually 2.5–5) dm high, with 1–3 nearly leafless stems, only the basal or nearly basal leaves being conspicuous, completely glabrous to glandular or hispidulous especially on the peduncles and involucre; root vertical, fleshy, simple, and deeply penetrating or forked, branched or \pm fibrous; caudex swollen, simple or 1-furcate, 1–3-stemmed; caudical leaves 3–30 (usually 7–15) cm long, 0.5–8 cm wide, elliptic or obovate to oblanceolate, lanceolate or linear, obtuse or acute, sessile or tapering into a short or long winged petiole, pinnatifid, runcinately toothed, denticulate or entire; cauline leaves much reduced, mostly lanceolate, linear or bractlike; stems erect, slender or sometimes stoutish, terete, striate or sulcate, sometimes simple, 1-headed, usually branched above the middle, occasionally from near the base, lower branches elongated, simple or branched above, forming a simple or compound corymbiform cyme; inflorescence of 1–30 heads; peduncles 1–15 cm long, slender, slightly enlarged and sulcate near the head; heads erect, small, medium or large, 20–50-flowered; involucre turbinate-campanulate, the outer bracts calyculate or sometimes imbricate, 8–21 mm long; outer bracts 5–12, lanceolate, to linear, appressed, unequal, the longest $\frac{1}{4}$ – $\frac{2}{3}$ as long as the inner; inner bracts 10–16 (18) lance-linear to broadly lanceolate, obtuse to acute or acuminate, glabrous on inner face, becoming dorsally carinate, spongy-thickened at the base in mature fruiting heads, ultimately reflexed; receptacle fimbriate, shortly ciliate; corollas 9–18 mm long; ligules 1.5–3 mm wide; corolla tube 4–6 mm long, glabrous or shortly pubescent; anther tube (4)5 \times 1.3 (1.5) mm dis.; appendages 0.6–1 mm long, narrow, oblong, acute or obtuse; style branches 1.5–3 mm long, yellow; achenes from light to very dark brown, fusiform, moderately attenuate to shortly and coarsely beaked, 3.5–7.5 mm long, 0.5–1 mm wide, 10–13-ribbed, ribs smooth or finely spiculate; pappus white, 4–8 mm long, the setae variable in different forms, from 2-seriate, free to the very base, equally fine and deciduous, to 4-seriate, united at the base, very unequal, the coarsest up to 60 μ wide at the base, and persistent. Flowering May–Aug.; flowers golden yellow. Chromosomes $2n = 22$.

Manitoba, W. Minnesota, Iowa, and Nebraska, southwestward in the mountains to N. New Mexico, and westward to E. California, Oregon, and Washington.

This is the most widespread and probably the most polymorphic of the American species of *Crepis*. The variation within the species as a whole is continuous, but

extreme variants occur. These are connected with the more common forms by intergradations. Although several of these more outstanding forms were previously described as species, extensive herbarium and field studies resulted in the reduction to synonymy of all but six of them. Since these six entities occupy rather well-marked geographic areas, and since their areas overlap and many intergrading forms occur, they are recognized as subspecies.

Key to the Subspecies of Crepis runcinata

Involucres strongly or slightly glandular-pubescent, at least toward the base.

Teeth of leaves not at all or only slightly white-tipped; involucre bracts linear or lanceolate, the outer less than 2 mm broad, usually conspicuously shorter than the inner.

Basal leaves narrowly obovate, elliptic, oblanceolate, lanceolate, or spatulate, mostly 0.5–3.5 cm broad and 4–8 times as long; inflorescence bearing 1–14, mostly 3–7, heads.

Leaves mostly green and remotely dentate, pinnatifid, or entire, contracted to a narrow, slightly alate petiole; achenes attenuate at the apex, but not beaked; Rocky Mountain reg. and eastward.....124, *a. typica*

Leaves glaucous, closely dentate, gradually narrowed to the broad, strongly alate petiolar base; achenes mostly strongly attenuate at the apex; E. California and W. Nevada.....124, *g. Hallii*

Basal leaves obovate, mostly 3–8 cm broad and 2–4 times as long; inflorescence bearing 9–30, mostly 12–25, heads.....124, *b. hispidulosa*

Teeth of leaves white-tipped; involucre bracts broadly lanceolate or elliptic, evenly imbricate, the outer 2–3 mm broad.

Involucres 19–21 mm high, their bracts attenuate at the apex; achenes with a short but distinct beak124, *j. Andersonii*

Involucres 10–13 mm high, their bracts abruptly contracted to the obtuse or acute apex; achenes beakless.....124, *e. imbricata*

Involucres not at all glandular.

Leaves narrowly obovate, oblanceolate, or spatulate, 1.5–4 cm broad and 4–8 times as long; involucres 8–12 mm high, the outer bracts minute, deltoid.....124, *c. glauca*

Leaves oblanceolate or linear, 0.6–1.5 cm broad and 9–20 times as long; involucres 14–16 mm high, the outer bracts elongated, lanceolate.....124, *d. Barberi*

124, *a. Crepis runcinata typica* Babc. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 93. 1938. Basal leaves narrowly obovate, elliptic, lanceolate or spatulate, 0.5–3.5 cm wide and 4–8 times as long, sessile, or with a petiole up to $\frac{2}{3}$ as long as the blade, remotely dentate, runcinate-pinnatifid or entire, green or occasionally glaucous, glabrous or \pm gland-hispidulous, margin sometimes ciliate; inflorescence of 1–12 (mostly 3–7) heads; peduncles glabrous or gland-puberulent; involucres 9–16 mm long, \pm gland-pubescent or hispid, sometimes tomentose; outer bracts deltoid or lanceolate, $\frac{1}{3}$ – $\frac{1}{2}$ or rarely $\frac{2}{3}$ as long as the inner; inner bracts lanceolate, \pm attenuate toward the apex; achenes 3.5–7.5 (mostly 4–5.5) mm long, \pm attenuate but not beaked. See fig. 177.

Hieracium runcinatum James, in Long's Exped. 1: 453. 1823.

Crepis biennis Hook., Fl. Bor. Am. 1: 297. 1834, non L.

C. biennis var. *americana* DC., Prod. 7: 163. 1838.

Crepidium runcinatum Nutt., Trans. Am. Phil. Soc. n.s. 7: 436. 1841.

Crepis runcinata Torr. et Gray, loc. cit.

Hieraciodes runcinatum O. Kuntze, Gen. 346. 1891.

Crepis runcinata alpicola Rydb., Bull. Torr. Bot. Club 24: 299. 1897.

C. alpicola Nelson, Bot. Gaz. 40: 65. 1905.

C. glauca Rydb., op. cit., 28: 512. 1901.

C. denticulata Rydb., op. cit., 32: 135. 1905.

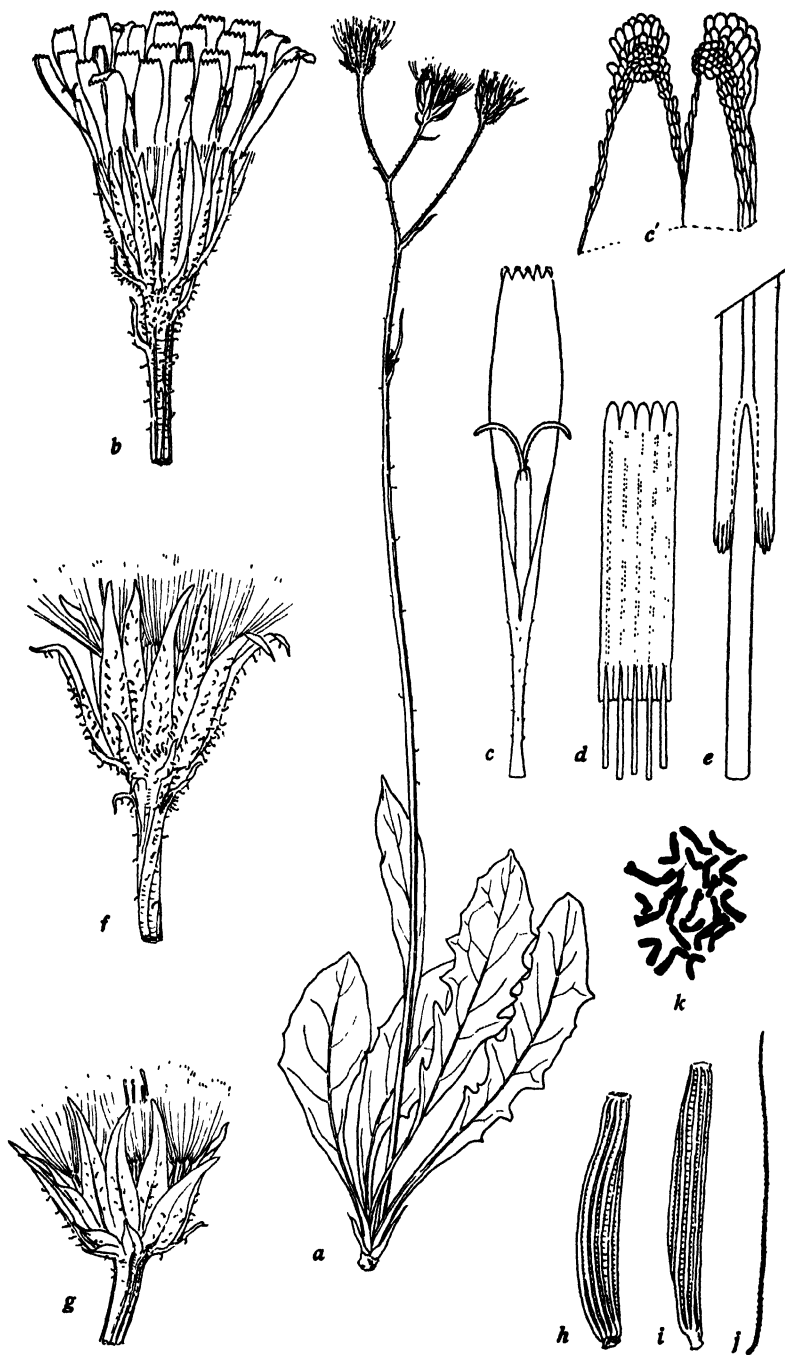


Fig. 177. *Crepis runcinata typica*, a, from Rydberg 840 (Minn 217884); b-e, from Moodie in 1913 (US 624688); f, from Moodie 921 (DS 65998); g-j, from Rydberg 217 (US 43412); k, from hort. genet. Calif. 2065 (plants collected at Red Rock Lake, Colo., Babcock 108, UC 346603): a, plant, $\times \frac{1}{2}$; b, flower head, $\times 2$; c, floret lacking ovary, $\times 4$; d, anther tube, $\times 8$; e, detail of ligule teeth, $\times 50$; f, g, fruiting heads, $\times 2$; h-j, achenes and a pappus seta, $\times 8$; k, somatic chromosomes, $2n = 22$, $\times 1250$.

- C. perplexans* Rydb. and *C. tomentulosa* Rydb., *ibid.*, 134. 1905.
C. dakotana Lunell, *Am. Midl. Nat.* 2: 289. 1912.
C. neomezicana Woot. et Standley, *Contr. U. S. Nat. Herb.* 16: 176. 1913.

Throughout the E. part of the range of the species, westward to Montana, Idaho, Utah, and New Mexico.

This subspecies is extremely variable; and, as the foregoing synonymy indicates, the recognition of several species has been proposed. But all attempts on the part of the present author to segregate from it entities distinguished by a set of recognizable characters and possessing a definite geographic range or ecological distribution were without success. For a discussion of the problem of variation in this subspecies and a more complete list of cited specimens, see Babcock and Stebbins (504: 94–96). The following specimens indicate both the geographic and morphologic range of the subspecies.

Without definite locality: Plains of the Platte, *Nuttall* in 1834 (PA, type). **Manitoba:** Oak R., Lothair, *Macoun and Herriot 42864* (NY, Mo, Po, FM). **Minnesota:** Chippewa Co., Montevideo, *Moyer* in 1896 and 1897 (US, Minn). **Saskatchewan:** Yorkton, *Herriot 42864* (G, NY, FM). **North Dakota:** Benson Co., Butte, *Lunell* in 1912 (US, type of *C. dakotana*; Minn). **South Dakota:** Pennington Co., Rochford, *Rydberg* in 1892 (US, G, NY). **Nebraska:** Cheyenne Co., Platte Bottom, *Rydberg 217* (US, NY). **Alberta:** near Banff, *Macoun* in 1891 (NY, Mo). **Montana:** Cascade or Meagher Co., Little Belt Mts., 2200 m, *Flodman* in 1896 (NY, type of *C. runcinata alpicola*; US). **Wyoming:** Carbon Co., Encampment, *Tweedy 4081* (NY, type of *C. perplexans*); Lincoln Co., Teton Forest Reserve, Pacific Creek, 2420 m, *Tweedy 603* (NY, type of *C. glauca*). **Colorado:** near Pikes Peak, Ruxton Dell, 2950 m, *Clements 342* (US, G, NY, Mo, RM, DS, type collection of *C. tomentulosa*); Jackson Co., North Park, *Shear and Bessey 4004* (NY, type of *C. denticulata*). **New Mexico:** Otero Co., Tularosa Creek, *Wootton* in 1896 (US, type of *C. neomezicana*). **Utah:** Juab Co., Juab, *Gooding 1087* (US, G, NY, Mo, UC).

124, b. *Crepis runcinata hispidulosa* (Howell) Bab. et Stebbins, *Carnegie Inst. Wash. Publ.* 504: 96. 1938. Leaves broader and more rounded at the apex than in subsp. *typica*, 6–25 cm long, 2.5–8 cm wide, mostly 2–3.5 times longer than wide; stem glabrous or gland-hispid; inflorescence of 10–30 heads; involucre 8–12 mm long, averaging slightly smaller than in subsp. *typica*, strongly or finely gland-hispid; achenes 3.5–5 mm long. See fig. 178.

- Crepis platyphylla* Greene, *Pittonia* 3: 27. 1896.
C. riparia Nelson, *Bull. Torr. Bot. Club* 26: 486. 1899.
C. runcinata var. *hispidulosa* Howell, *Mem. N. Y. Bot. Gard.* 1: 461. 1900.
C. petiolata Rydb., *Bull. Torr. Bot. Club* 32: 134. 1905, part.
C. riparia parva Nelson, *Man. Bot. Rocky Mts.*, 593. 1909.
C. aculeolata Greene and *C. pallens* Greene, *Leaflets Bot. Obs.* 2: 86. 1910.
C. obtusissima Greene, *op. cit.*, 87.

N.W. part of the range of the species, eastward to W. Montana, E. Idaho, and N.W. Colorado, where it intergrades with subsp. *typica*, southward to S. Oregon and N. Utah, where it intergrades with subsp. *glauca*. The following are typical specimens.

Montana: Central Park, *Brandege* in 1898 (UC); Helena, *Kelsey* in 1890 (Minn). **Colorado:** Routt Co., Steamboat Springs, *Gooding 1657* (US, G, NY, PA, Mo, RM, UC, DS). **Idaho:** Canyon Co., Emmett, 900 m, *MacBride 884* (DS, Minn, as *C. riparia*, *fide* Nelson); Bear Lake Co., Montpelier, *Greene* in 1889 (ND 48685, 48686, type collection of *C. platyphylla*). **Utah:** Rabbit Valley, 2000 m, *Ward 606* (US; another sheet of this collection, US 47205, without locality, is the type of *C. aculeolata*). **Washington:** Lincoln Co., Sprague, 550 m, *Sandberg and Leiberg 208* (UC, PA). **Oregon:** Harney Co., Stein's Mts., *Howell* in 1885 (US, G, NY, PA, DS, Or).

124, c. *Crepis runcinata glauca* (Nutt.) Bab. et Stebbins, *Carnegie Inst. Wash. Publ. No.* 504: 98. 1938. Leaves variable in size, as in subsp. *typica*, oblanceolate or lanceolate, entire, runcinately dentate or pinnately lobed, the petiole definitely

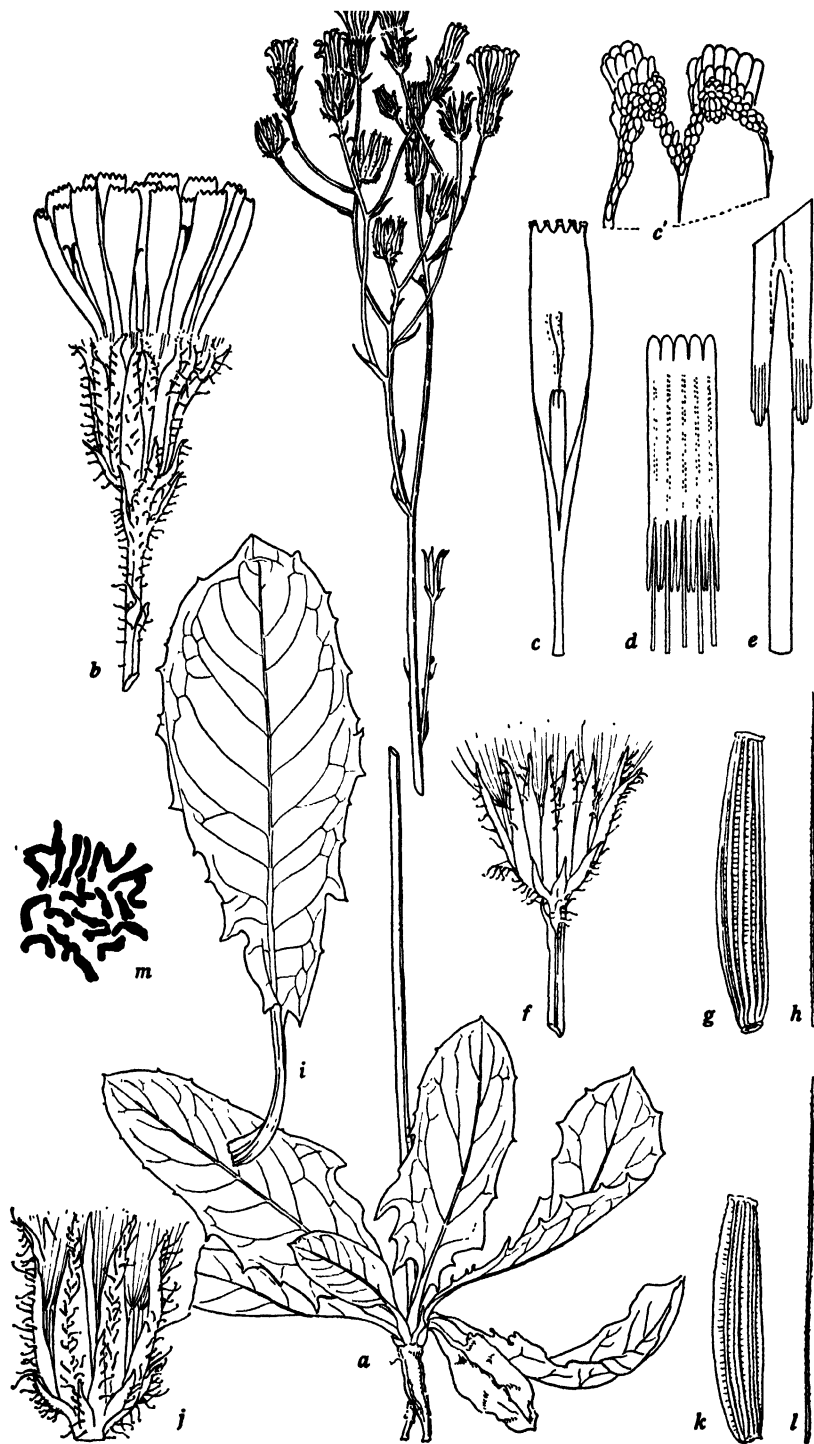


Fig. 178. *Crepis runcinata hispidulosa*, a-h, from Cusick 1713 (UC 31326); i-l, from Gooding 1657 (UC 70068); m, from hort. genet. Calif. 1829 (Babcock and Collins 50, 54, UC 296056, 7): a, plant, $\times \frac{1}{2}$; b, flower head, $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule teeth, $\times 50$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, fruiting head, $\times 2$; g, h, achene and pappus seta, $\times 8$; i, leaf, $\times \frac{1}{2}$; j, fruiting head, $\times 2$; k, l, achene and pappus seta, $\times 8$; m, somatic chromosomes, $2n = 22$, $\times 1250$.

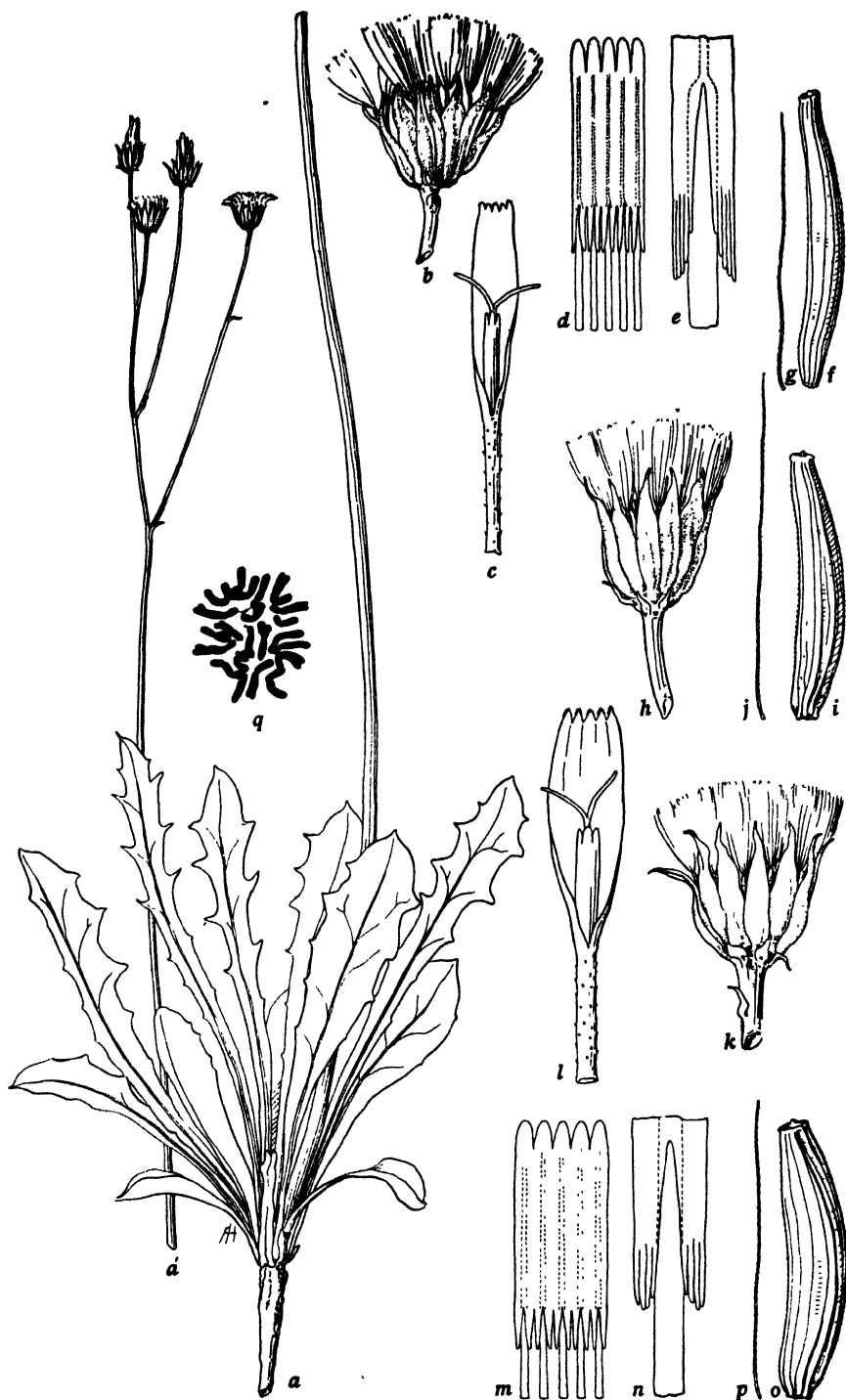


Fig. 179. *Crepis runcinata glauca*, a-g Greene in 1896 (UC 194361); h-j, from Garrett 1497 (DS 119718); k-q, from hort. genet. Calif. 27.2079, grown from roots collected at type locality of *C. chamaephylla* Woot. et Stand. (UC 676613): a, a', plant, $\times \frac{1}{2}$; b, head, $\times 2$; c, floret lacking ovary, $\times 4$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, g, achene and a pappus seta, $\times 8$; h, head, $\times 2$; i, j, achene and a pappus seta, $\times 8$; k, head, $\times 2$; l, floret lacking ovary, $\times 4$; m, anther tube, $\times 8$; n, detail of appendages, $\times 32$; o, p, achene and a pappus seta, $\times 8$; q, somatic chromosomes, $2n = 22$, $\times 1250$.

alate, glabrous and glaucous; stem, branches, and peduncles glabrous; inflorescence of 3–15 heads; involucre 7–12 mm high, averaging somewhat smaller than in subsp. *typica*, completely glabrous or lightly tomentulose on the inner bracts; outer bracts deltoid, less than $\frac{1}{4}$ as long as the inner, often pale or whitish; inner bracts lanceolate, \pm attenuate; achenes somewhat smaller than in subsp. *typica*, 3.5–5.5 mm long. See fig. 179.

Crepidium glaucum Nutt., Trans. Am. Phil. Soc. n.s. 7: 436. 1841.

C. caulescens Nutt., loc. cit.

Crepis glauca Torr. et Gray, Fl. N. Am. 2: 488. 1843.

Hieraciodes caulescens O. Kuntze, Gen. 345. 1891.

C. chamaephylla Woot. et Standley, Contr. U. S. Nat. Herb. 16: 175. 1913.

Saskatchewan to Idaho, southward to New Mexico and Arizona.

This subspecies is found sparingly in the N.E. part of the range of the species; but it is more common in Utah and Nevada. It grows in more alkaline situations than the two preceding subspecies. The following are typical.

Without definite locality: Plains of the Platte, *Nuttall* in 1834 (BM, type of *Crepidium glaucum*; UCf). **Saskatchewan:** Little Manitou Lake, *Macoun* and *Herriot* 42866 (NY, FM, Po). **South Dakota:** Harding Co., Cave Hills, *Visher* 402 (G, RM). **Montana:** Powell Co., Deer Lodge, *Jones* in 1905 (US, Po). **Wyoming:** Johnson Co., Buffalo, *Nelson* 2513 (Minn). **Colorado:** Delta Co., near Delta, *Osterhout* 6580 (Po). **Idaho:** Thousand Springs Valley, 2030 m, *Henderson* 3668, 3669 (US). **Utah:** Salt Lake Co., Beck's Hot Springs, 1360 m, *Garrett* 1497 (US, G, PA, DS); Juab Co., Juab, *Gooding* 1089 (US, Po); Piute Co., above Marysville, *Eydeberg* and *Carlton* 6923 (US, G, NY, RM, Nev). **Nevada:** Elko Co., Ruby Valley, *Heller* 9474 (US, NY, PA, Mo); Nye Co., near Currant, *Bentley* in 1916 (DS, Po). **Arizona:** N. end of Carrizo Mts., *Standley* 7419 (US, type of *C. chamaephylla*).

124, *d. Crepis runcinata Barberi* (Greenm.) Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 100. 1938. Basal leaves 10–20 cm long, 0.5–2 cm wide, narrowly oblanceolate, retrorsely dentate or pinnatifid with lanceolate lobes, glabrous and \pm glaucous; stems 3.5–6.5 dm high; inflorescence of 3–7 heads; involucre 11–17 mm long, completely glabrous; outer bracts narrowly lanceolate, the longest about $\frac{1}{2}$ as long as the inner; inner bracts conspicuously scarious-margined; achenes dark brown, 5.5–7 mm long; pappus 7–8 mm long. See fig. 180.

Crepis Barberi Greenm., Proc. Am. Acad. 40: 52. 1904.

C. mogollonica Greene, Contr. U. S. Nat. Herb. 16: 176. 1913.

W. New Mexico in the Mogollon Mts.; and in the state of Chihuahua, Mexico, in the Sierra Madre.

This subspecies does not possess any characteristics, other than the extremely narrow leaves, which set it off sharply from the preceding. The involucre is glabrous, as in subsp. *glauca*, but the outer involucral bracts are longer, as in certain specimens from Colorado which are intermediate between subsp. *glauca* and subsp. *typica*. The involucre and achenes of the Mexican specimens are unusually large for *C. runcinata*; but they are equaled by those of some forms from Colorado, and the collection from New Mexico is intermediate in this respect. A transitional variant, collected in the White Mts. of Arizona, *Griffiths* 5354 (US), has the narrow leaves of subsp. *Barberi*, but the involucre is as in subsp. *glauca*. The following specimens of this subspecies have been seen.

Mexico: Sierra Madre Mts., near Colonia Garcia, 2285 m, *Townsend* and *Barber* 206 (G, type of *C. Barberi*; US, Mo, Po); Sierra Madre, *Nelson* 6107 (G, US); Sierra Madre, Mound Valley, 2120 m, *Jones* in 1903 (Po). **New Mexico:** Catron ("Socorro") Co., Mogollon Mts., W. fork of Gila R., 2420 m, *Metcalf* 576 (US, type of *C. mogollonica*; Minn).

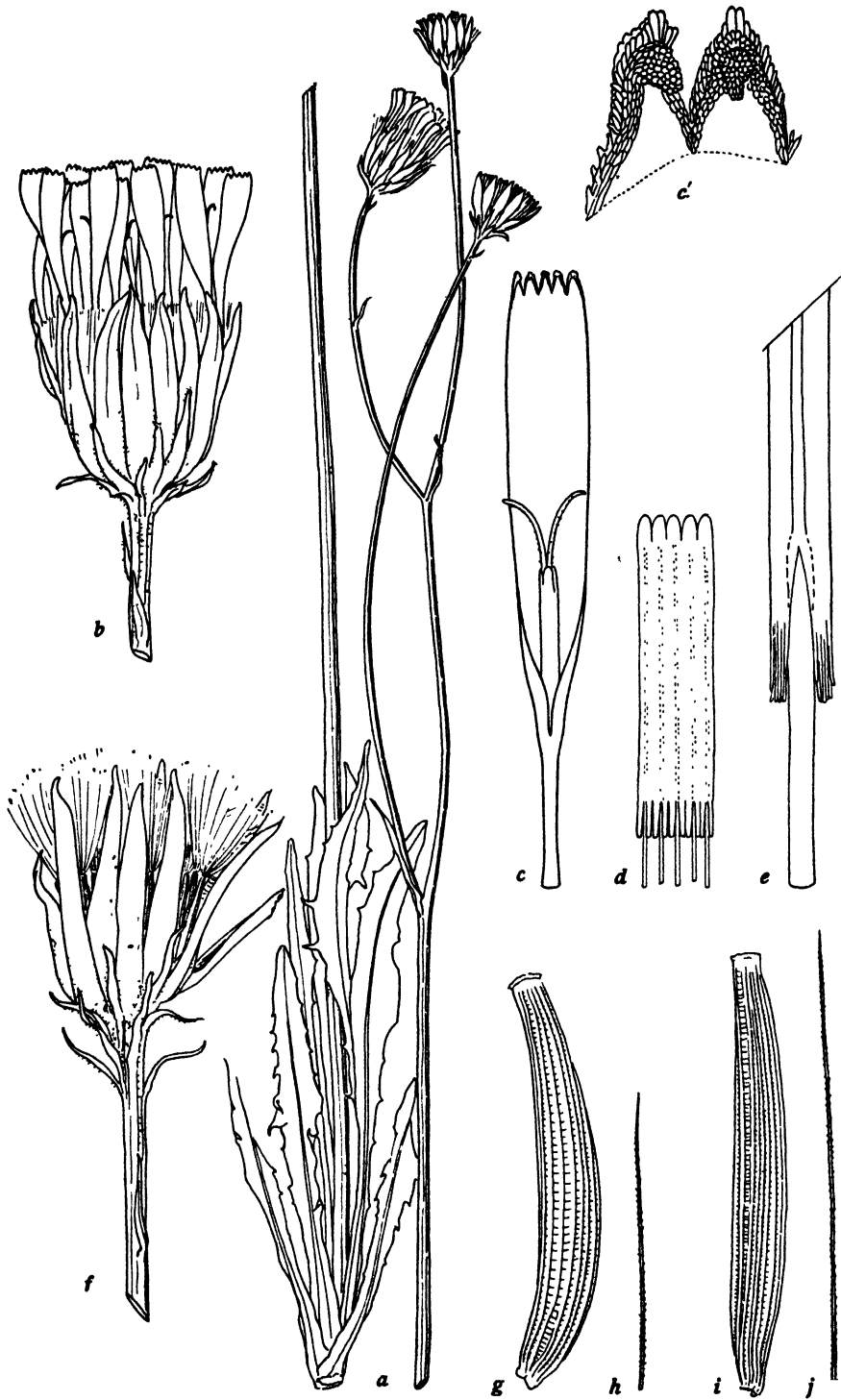


Fig. 180. *Crepis runcinata* Barberi, a-c, from type collection (US 347084); f-i, from M. E. Jones in 1903 (Po): a, plant, $\times \frac{1}{2}$; b, flower head, $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule teeth, $\times 50$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, fruiting head, $\times 2$; g-j, achenes and pappus setae $\times 8$.

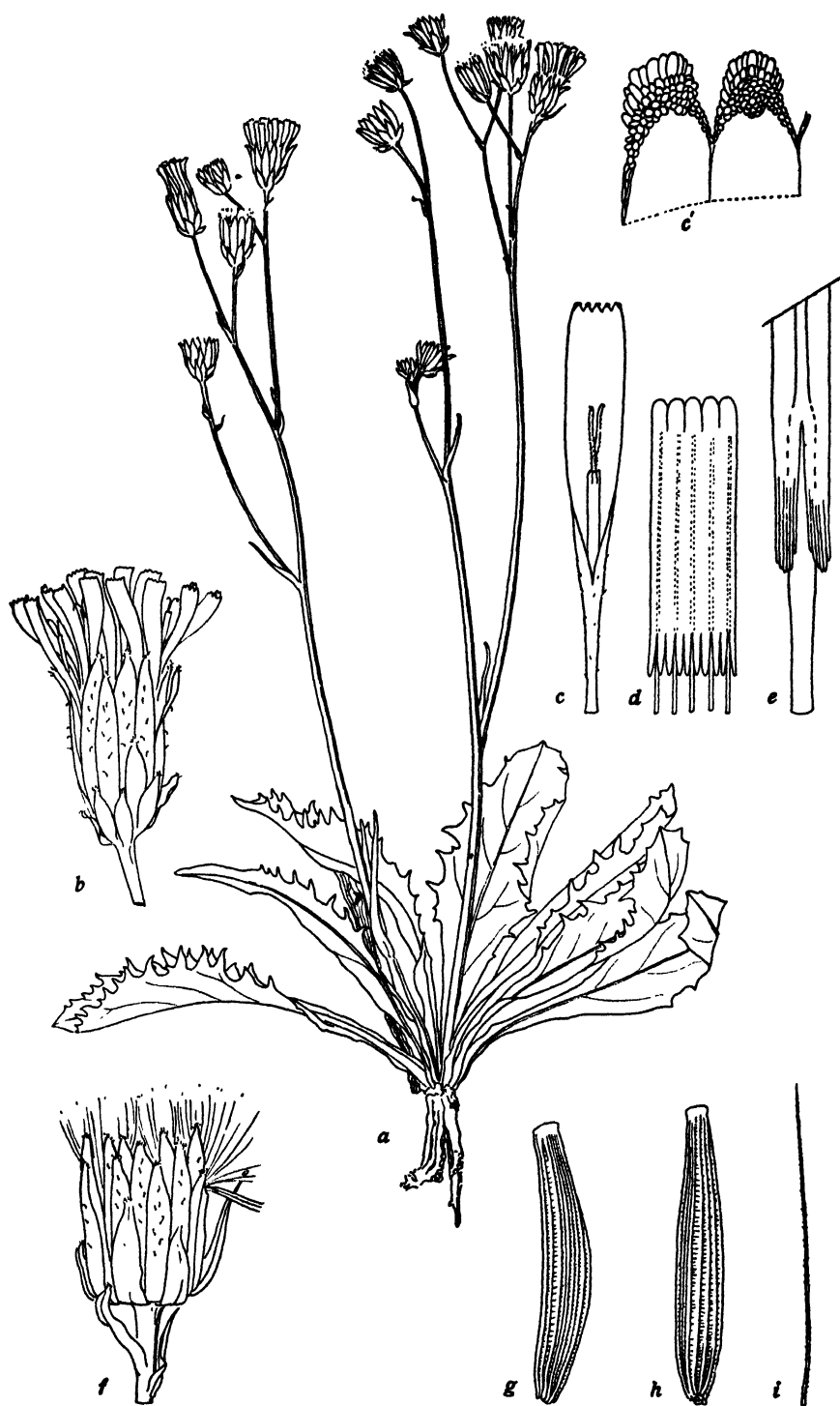


Fig. 181. *Crepis runcinata imbricata*, *a-e*, from type and isotype, *Cusick 2014* (Minn 217746); *f-i*, from *Eastwood 14853* (CA 146244): *a*, plant, $\times \frac{1}{2}$; *b*, flower head, $\times 2$; *c*, floret lacking ovary, $\times 4$; *c'*, detail of ligule teeth, $\times 50$; *d*, anther tube, $\times 8$; *e*, detail of appendages, $\times 32$; *f*, fruiting head, $\times 2$; *g-i*, achenes and pappus seta, $\times 8$.

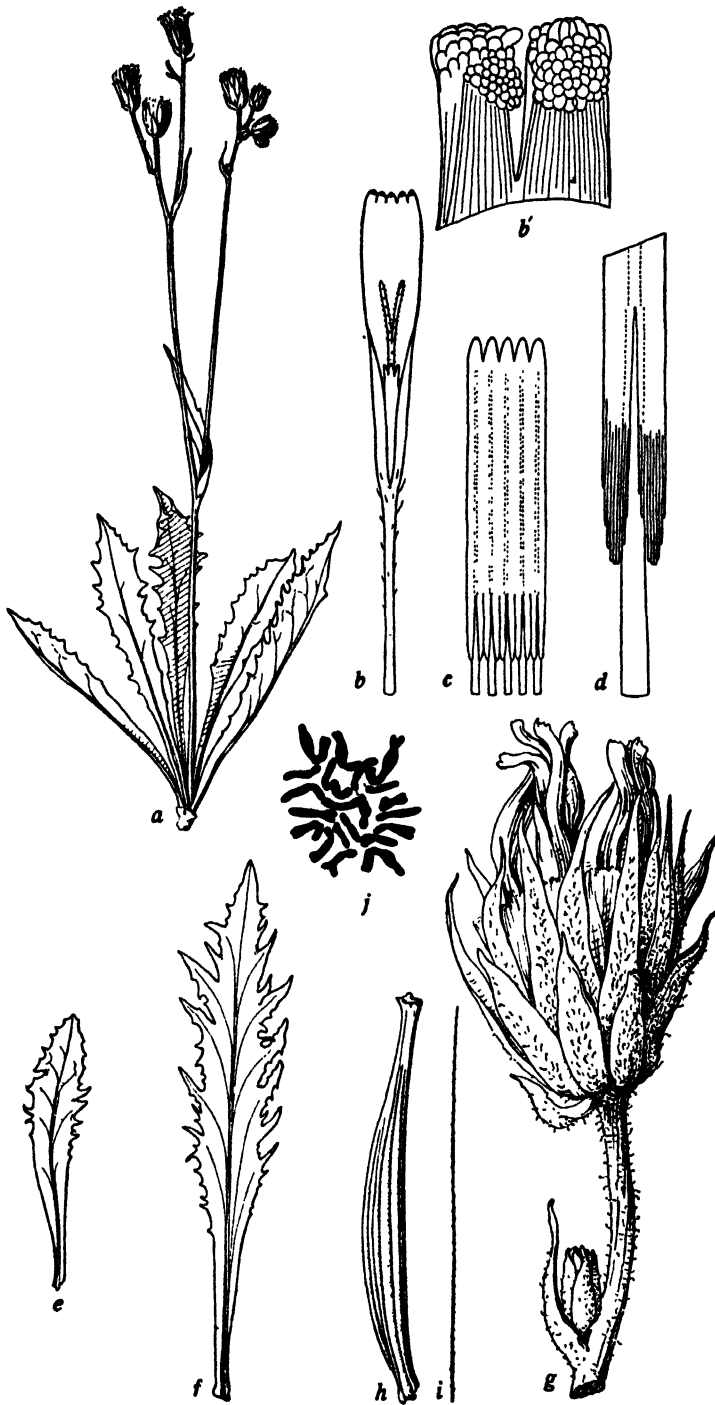


Fig. 182. *Crepis runcinata* Andersonii, a-d, from Baker 1062 (UC 135440); e-i, from type collection (G); j, from hort. genet. Calif. 2086 (roots collected at type locality, Babcock 120): a, plant, $\times \frac{1}{4}$; b, floret lacking ovary, $\times 4$; b', detail of ligule teeth, $\times 50$; c, anther tube, $\times 8$; d, detail of appendages, $\times 32$; e, f, caudical leaves, $\times \frac{1}{2}$; g, head in anthesis, $\times 2$; h, i, achene and a pappus seta, $\times 8$; j, somatic chromosomes, $2n = 22$, $\times 1250$.

124, *e. Crepis runcinata imbricata* Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 102. 1938. Leaves 5–11 cm long, 1.5–3 cm wide, oblanceolate or elliptic, strongly and closely dentate, the teeth conspicuously corneous-mucronate; stems 1.5–3 dm high; inflorescence of 3–7 heads; involucre 10–11 mm long, gland-pubescent; inner bracts oblong, shortly attenuate near the apex, obtuse and ciliate at the tip; outer bracts similar, 2–3 mm wide, very unequal, the longest about $\frac{2}{3}$ as long as the inner; achenes reddish-brown, 4.5–5 mm long, attenuate but not at all rostrate; pappus 5–7 mm long. See fig. 181.

S. Oregon to N. and W. Nevada, in alkaline meadows.

This subspecies resembles subsp. *Andersonii* in its leaves and in the broad, strongly imbricate bracts of the involucre; but the heads are the same size as those of subsp. *typica*; and the achenes are not at all beaked. The following specimens have been seen.

Oregon: Harney Co., Alvord Valley, *Cusick 2014* (UC 31293, type; G, Minn); near Alvord Lake, 1300 m, *Leiberg 2529* (UC, G); Harney Co., near Alberson, *Peck 14019* (Will); Lake Co., north of Adel, *Peck 19487* (UC, Will). **Nevada:** Washoe Co., Steamboat Springs, *Eastwood 14853* (CA); Washoe Co., Lemmon Valley, *Kennedy 2061*, part (UC); Elko Co., east of Elko, *Eastwood and Howell 276* (CA).

124, *f. Crepis runcinata Andersonii* (Gray) Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 104. 1938. Leaves as in subsp. *imbricata*, but often larger, glabrous or hispidulous on both sides; stems mostly robust, 2.5–5 dm high; inflorescence generally with 6–20 heads; involucre 13–21 mm long, gland-pubescent; inner bracts rather strongly attenuate to the apex; outer bracts similar, 2–3 mm wide, very unequal, the longest about $\frac{2}{3}$ as long as the inner; achenes pale yellow to reddish-brown, 6–8 mm long, shortly but \pm definitely rostrate, or merely attenuate; pappus 6–9 mm long. See fig. 182.

Crepis Andersonii Gray, Proc. Am. Acad. 6: 553. 1865.

W. Nevada and adjacent California, in damp alkaline meadows.

This subspecies is by far the most marked segregate in *C. runcinata*; but specimens now available indicate that it intergrades with other subspecies at the limits of its range. Although the beaked achenes have been generally regarded as sufficient to distinguish it from all of its relatives, there is every gradation from truly beaked achenes to those merely attenuate at the apex, even in plants otherwise typical of subsp. *Andersonii*; and, furthermore, definite beaks occur in some plants, cited in this paragraph, which have involucre typical of subsp. *typica*. The large involucre are also in their most typical form strikingly different from those of subsp. *typica*, but the specimens from Purdy and from Washoe County show intergradation in this respect. The following may be considered transitional forms (cf. *C. subcarnosa* Greene, Pittonia 3: 107. 1896; *C. runcinata ciliosa* Greene, *ibid.*, ex descr.): Nevada—Washoe Co., Lemmon Valley, *Kennedy 2061*, part (UC) involucre transitional from subsp. *Andersonii* to subsp. *imbricata*; Humboldt Wells, *Greene* in 1893 (UC, type of *C. subcarnosa* Greene), leaves and achenes as in subsp. *Andersonii*, involucre more as in subsp. *typica*; the whole plant densely hispidulous. The following specimens are typical of subsp. *Andersonii*.

Nevada: Ormsby Co., near Carson City, *Anderson in 1865* (G, type; US); about Carson City, 1446 m, *Baker 1062* (G, UC); Washoe Co., Reno, *Brandege* in 1883 (UC); Washoe Lake, *Bryant* (UC); Esmeralda Co., Soda Springs, *Shockley 266* (G, UC, DS). **California:** Sierra Co., *Lemmon* in 1874 (G); Sierra Co., Loyalton, *Eastwood 7792* (CA); Sierra Co., Purdy, *Heller and Kennedy 8666* (G, UC, DS, Nev).

124, *g. Crepis runcinata Hallii* Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 504: 104. 1938. Leaves glaucous, 6.5–27 cm long, 1.5–3 cm wide, oblanceolate

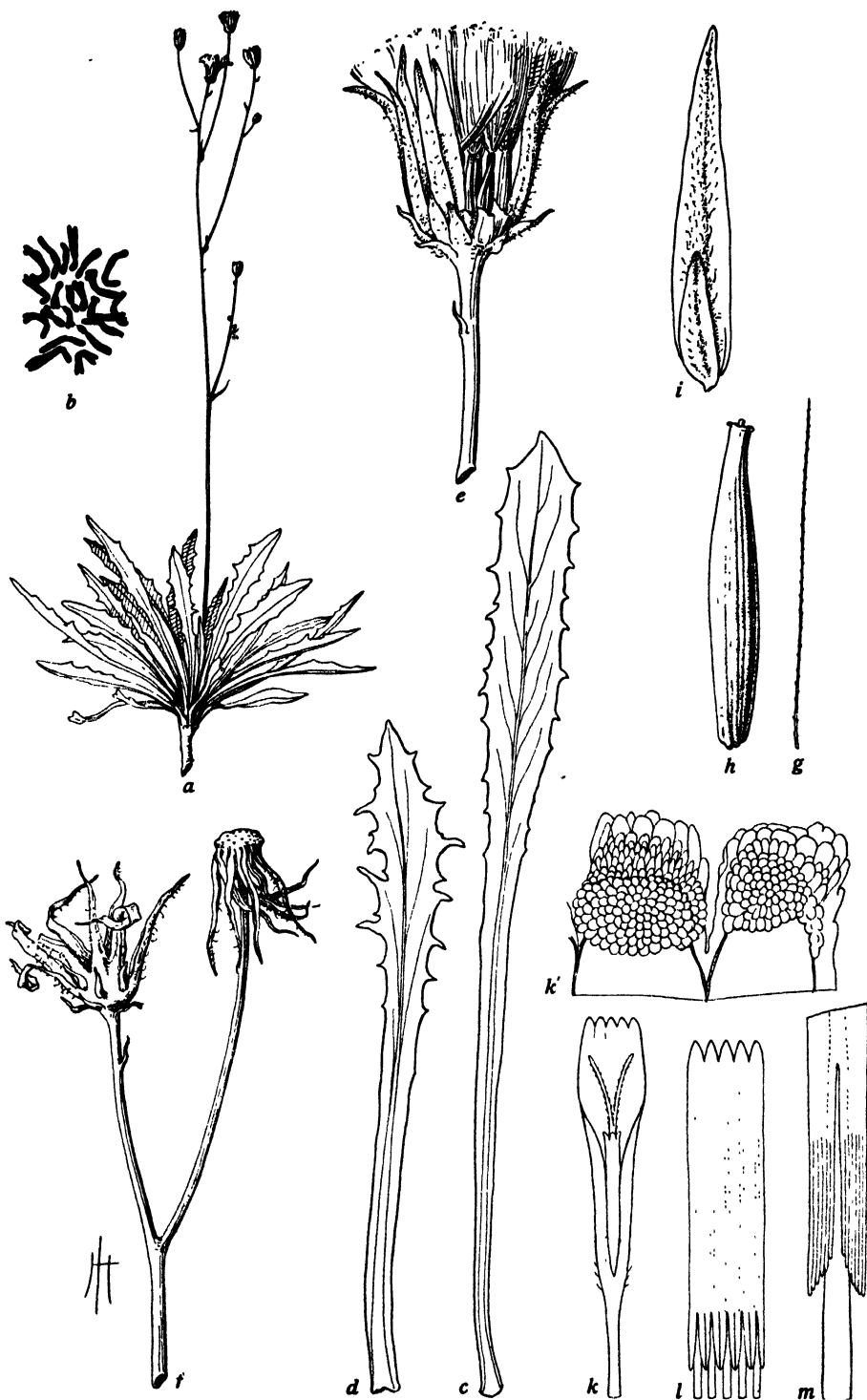


Fig. 183. *Crepis runcinata* Hallii, a, b, from Hall 11824 (hort. genet. Calif. 2136, UC 219418): c-i, from type (UC 313846); k-m, from Linsdale 624 (UC 499378): a, plant, $\times \frac{1}{4}$; b, somatic chromosomes, $2n=22$, $\times 1250$; c, d, caudal leaves, $\times \frac{1}{2}$; e, fruiting head, $\times 2$; f, old heads and peduncles, $\times 2$; g, h, achene and a pappus seta, $\times 8$; i, outer and inner involucrel bract, outer face, $\times 4$; k, floret lacking ovary, $\times 4$; k', detail of ligule teeth, $\times 50$; l, anther tube, $\times 8$; m, detail of appendages, $\times 32$.

or narrowly obovate, gradually narrowed to a long broadly winged petiole; closely and coarsely dentate or subpinnatifid; stems 2–6 dm high; inflorescence of 5–14 heads on elongated strict peduncles; involucre 9–13 mm long, gland-puberulent; outer bracts lance-deltoid, the longest about $\frac{1}{2}$ as long as the inner; inner bracts 1.2–1.8 mm wide, lanceolate, acute; achenes chestnut brown, 4.5–6.5 mm long, strongly or moderately attenuate to the apex; pappus 6–7 mm long. See fig. 183.

E. California to central Nevada.

This subspecies occurs south of the range of subsp. *Andersonii* and west of that of subsp. *glauca*. In morphologic characters, as well as in geographic distribution, it is intermediate between these two subspecies. Although most of the specimens have the achenes strongly attenuate to the apex, they are not as definitely beaked as in most forms of subsp. *Andersonii*; furthermore, the involucre is much smaller and the bracts are narrower. Specimens like those of Blake from Bridgeport (see below) having only moderately attenuate achenes are difficult to distinguish from subsp. *typica*. The relatively long and narrow glaucous leaves with broadly winged petioles, however, are distinct from most forms of subsp. *typica*. Also, the wide gap in the range of the two subspecies and their different ecological habitats are additional reasons for recognizing subsp. *Hallii*. The following have been seen.

California: Mono Co., Benton, in *Distichlis* sod, *Hall 12281* (UC 313486, type); north of Benton, Adobe Valley, *Hall 11824* (UC); Inyo Co., Bishop, *Davidson 2570* (UC); near Bishop, *Jones* in 1927 (Po); Mono Co., Bridgeport, *Blake 11837* (UC). **Nevada:** Lander Co., between Battle Mountain and Austin, 1950 m, *Hitchcock 698* (US); Nye Co., southeast of Millet, 1660 m, *Linsdale 613, 624* (UC); Esmeralda Co., White Mts., Trail Creek, 2530 m, *Duran 2501* (UC).

Relationship

Crepis runcinata, as was pointed out by Babcock and Stebbins (*op. cit.*, p. 30), is sufficiently similar to *C. praemorsa* of E. Siberia and *C. gymnopus* of N. Japan, both with 4 pairs of chromosomes, to suggest that the three species had a common ancestor. No species is known which might have been the 7-paired ancestor of *C. runcinata*.

SECTION 16. LAGOSERIS

The 5 species in this section are characterized by having the receptacle paleaceous, the achenes uniform, and the root perennial. There is considerable variation within the species, however, with respect to type of root and size and habit of the plant. In *C. connexa* the type of root is not known with certainty, but apparently

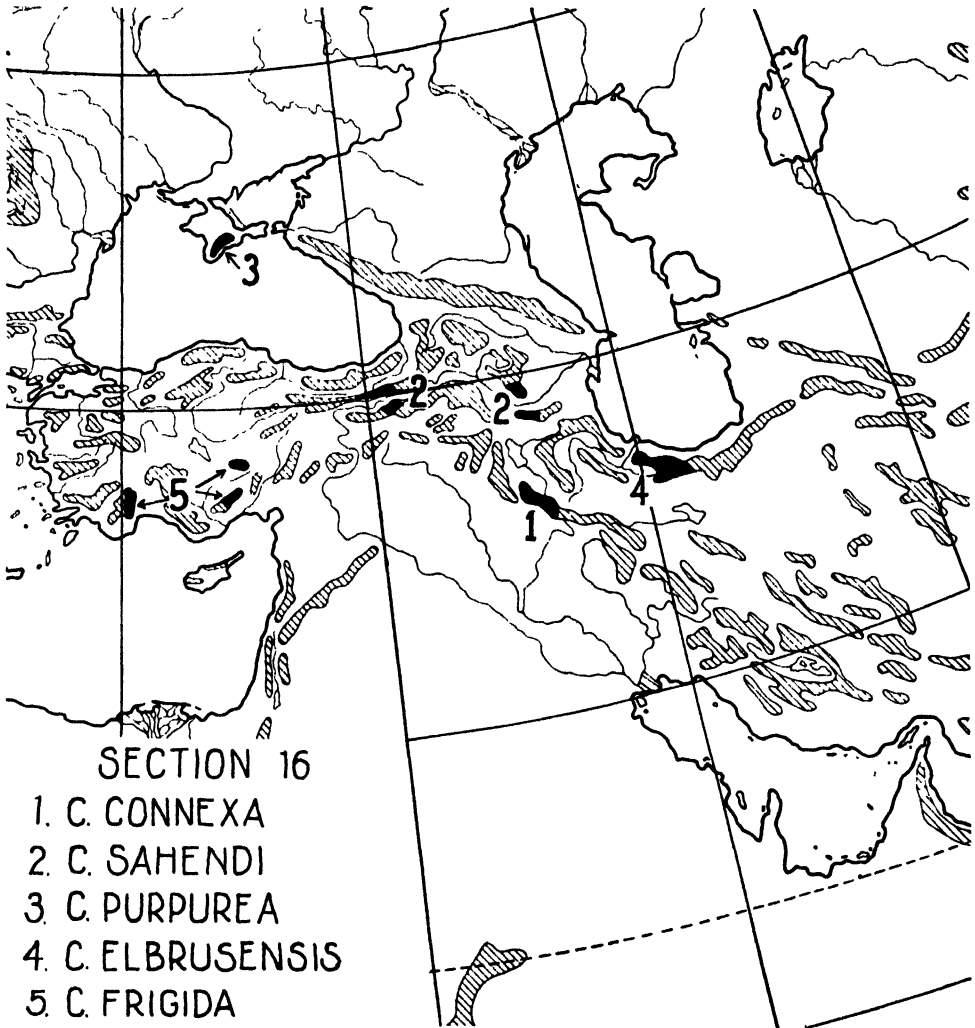


Fig. 184. Geographic distribution of the 5 species in sec. 16. Their restricted distributions are indicated by the solid black areas, the shaded areas being mountain ranges or masses. Based on Goode Base Map No. 124. By permission of the University of Chicago Press.

it is deeply penetrating, as in *C. sahendi* (see fig. 186). In *C. purpurea* the caudex is elongated into a horizontal or oblique subterranean stem bearing fleshy fibers. In *C. elbrusensis* the caudex is subterranean, but it is elongated, deeply penetrating and rootlike, whereas in *C. frigida* the plant spreads by stolonlike, slender shoots arising from buds on the deeply penetrating caudex. Thus, in this one section are exemplified most of the different types of subterranean growth found throughout the genus. The variation in size of plant is also very great, ranging from a height

of 4.5 dm in *C. connexa* down to about 0.5 dm in *C. frigida*. In habit the first four species are characterized by a branched, though few-headed, stem; whereas in *C. frigida* the stems are all scapiform. Other differences might be mentioned. Nevertheless, it seems very probable that these five species all descended from a few very close species which in turn arose from a common ancestor. In addition to the common characteristics mentioned above, it should be noted that the receptacular paleae are always setiform, and there is considerable similarity in the floral morphology, particularly in size of corolla, anther tube, and appendages, and in the pappus setae, which are fine and soft. Furthermore, *C. connexa* is recognized definitely as a bridging species, since it exhibits considerable resemblance in habit of the plant, the leaves, and involucre to *C. songorica* and *C. sonchifolia* of sec. 10. One of these two species is endemic in Turkestan and the other in the Caucasus. The distribution of sec. 16 (fig. 184) is consistent with the hypothesis that these species were derived from the same line as sec. 10; and it indicates that the progenital species, from which these present-day species evolved, was widely distributed in S.W. Asia, and that spatial isolation has been an important factor in the evolution of these species.

Key to the Species of Section 16

- Cauline leaves several, large; involucre 12–15 mm long, 6–10 mm wide; style branches 2.5 mm long; achenes 7–8.5 mm long. 125. *C. connexa*, p. 618
- Cauline leaves few, bractlike; involucre 9–12 mm long, 3–6 mm wide; style branches 1–1.5 mm long; achenes 4.5–7 (mostly 5–6) mm long.
- Stems shaftlike, branched near the summit; leaves canescent-tomentulose or glabrous or finely pubescent with very short yellow hairs.
- Leaves glabrous or pubescent with short fine yellow hairs; corolla 16 mm long; anther tube 5 mm long; style branches yellow; achenes stramineous, 6–7 mm long, 0.6–0.7 mm. wide, 20-ribbed. 126. *C. sahendi*, p. 620
- Leaves canescent-tomentulose; corolla 11–12 mm long; anther tube 3.75 mm long; style branches green; achenes dark brown, 4.5–5 mm long, 0.5–0.6 mm wide, 10-ribbed. 127. *C. purpurea*, p. 622
- Stems low, branched near the base or scapiform; leaves densely pubescent with white or yellow setules.
- Leaves pubescent with white glandless setules; longest outer involucre bracts about $\frac{1}{3}$ as long as the inner; achenes stramineous, the marginal longer and wider than the inner. 128. *C. elbrusensis*, p. 626
- Leaves pubescent, especially on the lower face, with yellow setules; longest outer involucre bracts $\frac{1}{3}$ – $\frac{2}{3}$ as long as the inner; achenes light brown, all about the same size. 129. *C. frigida*, p. 628

125. *Crepis connexa* nom. nov.

(Fig. 185.)

Perennial, 4.5 dm high; caudex slender, woody, simple or divided at summit; caudal leaves few, ascending, up to 20 cm long, 4 cm wide, oblanceolate, acute, gradually attenuate into a long-winged petiole, entire, finely gland-pubescent on both sides; lower cauline leaves similar, middle cauline leaves up to 12 cm long, 4 cm wide, lanceolate, acute, sessile, subamplexicaul to auriculate-amplexicaul, denticulate to coarsely runcinate-dentate, sparsely pubescent or glabrescent; stem erect, terete, faintly striate, glabrous, paniculately 1–4-branched from below or above the middle, branches remote, divaricately ascending, pedunculate or 2-headed; peduncles 4–20 cm long, stout, arcuate, \pm swollen toward summit, strongly constricted just below the head, 1–2-bracteate, glabrous; heads erect, rather large,

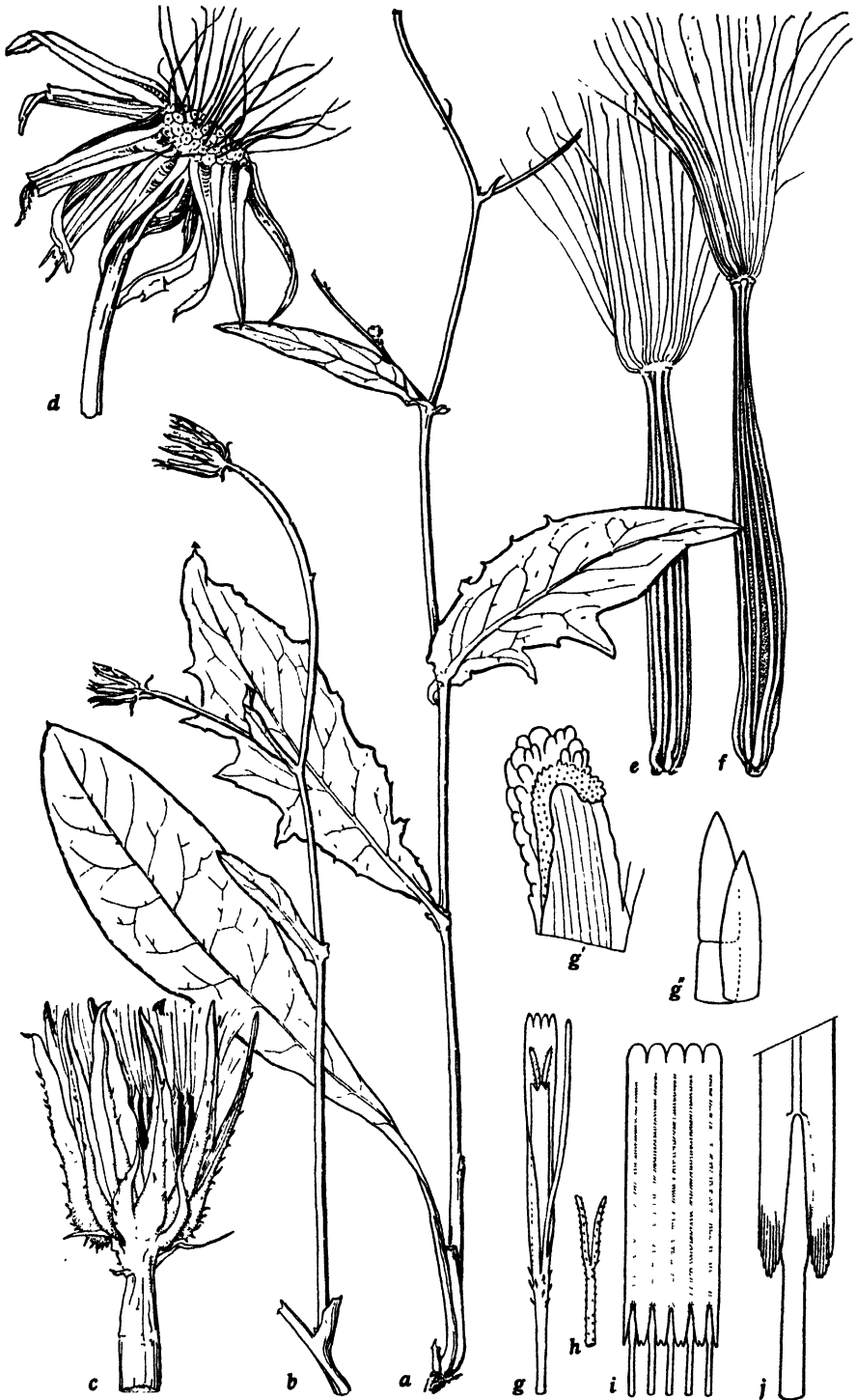


Fig. 185. *Crepis conneza*, from type (Bo): a, stem, with basal and cauline leaves, $\times \frac{1}{2}$; b, flowering branch, $\times \frac{1}{2}$; c, fruiting head, $\times 2$; d, old head, showing paleae, $\times 2$; e, f, marginal and inner achenes, $\times 8$; g, floret lacking ovary, $\times 4$; g', detail of ligule tooth, $\times 50$; g'', trichomes on corolla tube, $\times 50$; h, part of style, with branches, $\times 4$; i, anther tube, $\times 8$; j, detail of appendages, $\times 32$.

many-flowered; involucre campanulate to cyathiform, 12–15 mm long, 6–10 mm wide at middle in fruit, ultimately reflexed; outer bracts 5–6, unequal, longest $\frac{1}{2}$ – $\frac{2}{3}$ as long as inner bracts, linear, acute, like the inner bracts scarious toward base and black near apex, with a median dorsal row of short coarse setae; inner bracts 12–14, lanceolate, acute, becoming strongly carinate dorsally and spongy-thickened toward base in fruit, glabrous on inner face; receptacle nearly flat, alveolate with low membranous walls, each alveole subtended by a setiform palea, the paleae longer than the achenes, not exceeding the pappus; corolla about 13 mm long; ligule 2-parted, the main part about 1 mm wide and 4-toothed, the smaller segment 0.25 mm wide, 1-toothed; teeth 0.5 mm long, gland-crested, anteriorly labiate; corolla tube about 4 mm long, pubescent near summit with very stout several-celled simple or compound trichomes (somewhat like those of *C. sonchifolia*); anther tube 5.5×1.5 mm dis., appendages about 0.7 mm long, oblong, acute, united; filaments 0.5 mm longer; style branches 2.5 mm long, 0.2 mm wide, attenuate at tip, yellow; achenes uniform, light brown, 7–8.5 mm long, subterete, \pm attenuate toward summit, with slightly expanded pappus disk, constricted at the oblique pale-calloused base, 10-ribbed, the ribs rather prominent, rounded, muriculate, extending to pappus disk; pappus white, 4–5 mm long, 1–2-seriate, rather fine, soft, deciduous. Flowering June; flowers yellow.

Lagoseris hieracioides Boiss. et Haussk., ex Boiss., Fl. Orient. 3: 883. 1875.

N.W. Persia, mountains of Kurdistan, at 1830 m alt., on calcareous rocks. The only locality given by the collector that I have been able to locate is Avroman Dagh, which is on the Persian-Iraq frontier.

Monomorphic.

Persia: Kurdistan, Schahu Mts., *Haussknecht* 621 (Bo, UCf) type; Kurdistan, Avroman Mts., and Schahu Mts., *Haussknecht* in 1867 (B).

Relationship

C. connexa, as its name implies, must be considered as a bridging species. It connects this section and sec. 10, since it is obviously related to *C. sonchifolia* and *C. songorica*. The pollen grains of *C. connexa* are 3-pored and fairly regular in size, indicating that it is a diploid species; but the size is rather large, 30–37.5 μ in diameter, average 34 μ . It is certainly the most primitive *Crepis* species with a paleaceous receptacle; and it is considered to be a connecting species between sections *Lagoseris* and *Pterotheca*, on one hand, and the more primitive epaleaceous sections, on the other.

126. *Crepis sahendi* Boiss. et Buhse

Nouv. Mem. Soc. Nat. Mosc. 12: 141. 1860. (Fig. 186.)

Perennial, 1.5–3 dm high; caudex 0.5–3 cm wide, simple or 1–4-divided, woody, covered with dark brown bases of old leaves, prolonged into a straight slender taproot, leafy at summit; caudical leaves ascending, 3–12 cm long, 0.8–3 cm wide, oblanceolate, acute or acuminate, dentate to runcinate-pinnatifid with narrow acute often salient lateral segments, gradually attenuate into a narrowly winged petiole, broader at base, glaucous, glabrous or finely pubescent with very short yellow hairs; cauline leaves few, bractlike; stems 1–6, slender, erect, terete, striate, glabrous, cymosely 1–2-furcate near summit, branches pedunculate; peduncles 1–7 cm long, slender, arcuate, glabrous or sparsely pubescent near head; heads erect, medium, many-flowered; involucre cylindric-campanulate, 9–12 mm long, 4–6 mm wide at middle in fruit, \pm pubescent with pale yellow curled glandless hairs; outer bracts 10–12, unequal, $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner, lanceolate, acute; inner bracts 13–17,

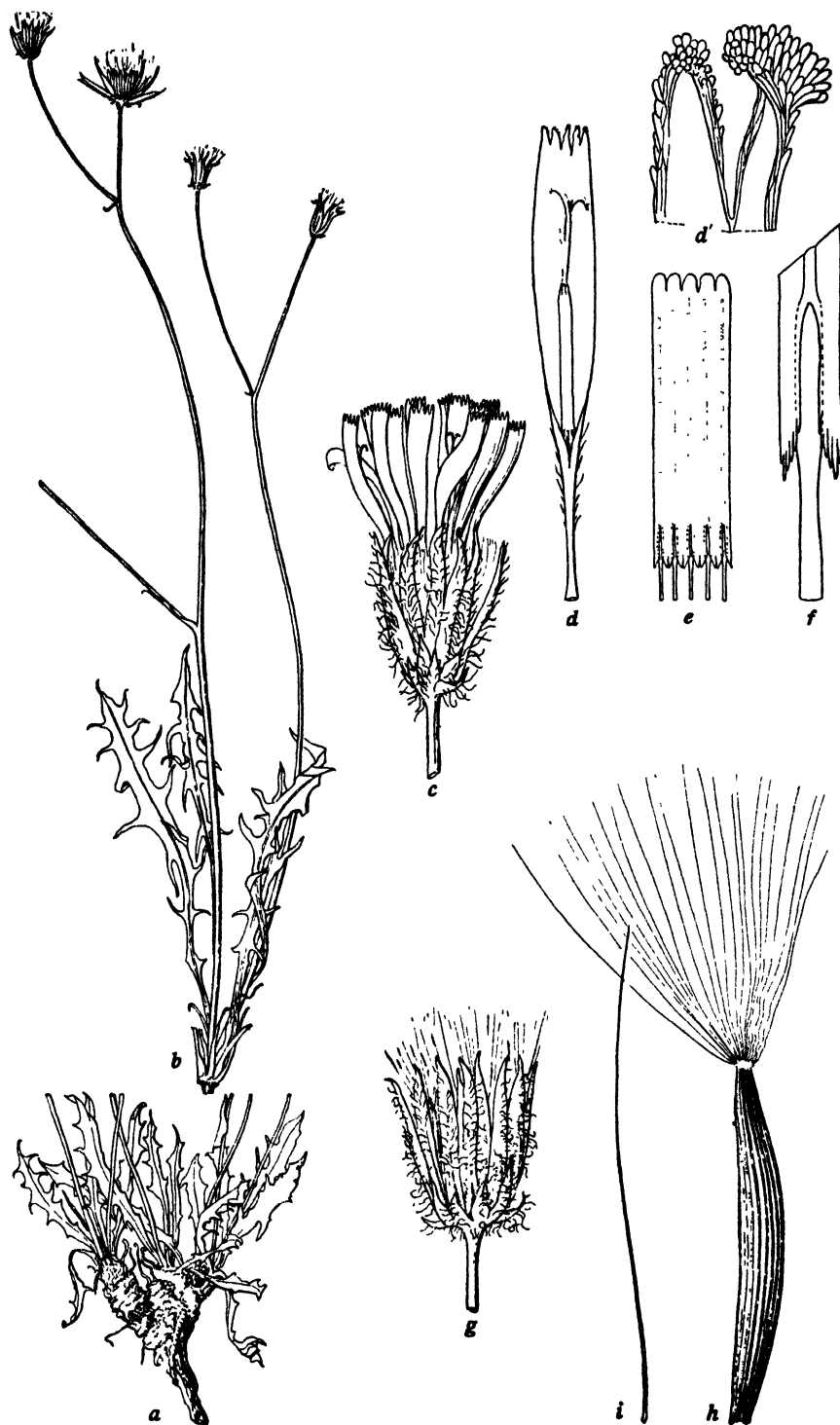


Fig. 186. *Crepis sahendi*, from Kotschy 500 (B, Bo): a, b, plants, $\times \frac{1}{2}$; c, flower head, $\times 2$; d, floret lacking ovary, $\times 4$; d', detail of ligule teeth, $\times 50$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, fruiting head, $\times 2$; h, i, achene and a palea from receptacle, $\times 8$.

lanceolate, acute, ventrally glabrous, dorsally becoming rounded-carinate and spongy-thickened at base in mature fruiting heads; receptacle paleaceous, the paleae yellow, setiform, longer than the achenes, not exceeding the pappus; corolla 16 mm long; ligule 1.75–2.5 mm wide; teeth 0.3–1 mm long, gland-crested; corolla tube 4.5 mm long, sparsely pubescent with coarse straight several-celled trichomes 0.5 mm long; anther tube 5×1.2 mm dis.; appendages 0.75 mm long, oblong, sagittate; filaments 0.5 mm longer; style branches about 1.5 mm long, 0.2 mm wide, obtuse, yellow; achenes monomorphic, stramineous, 6–7 mm long, 0.6–0.7 mm wide, fusiform, nearly equally attenuate to both ends, with slightly expanded pappus disk, lightly calloused at the hollow base, about 20-ribbed, ribs weak, narrow, rounded, smooth; pappus white, 4.5–5 mm long, 2–3-seriate, rather fine, soft, persistent. Flowering June–Aug.; flowers yellow.

Crepis Huetti Boiss., Fl. Orient. 3: 838. 1875.

Pterotheca runcinata Trautv., Acta Hort. Petrop. 4: 385. 1876.

Lagoseris runcinata Boiss., Fl. Or. Suppl. 329. 1888.

Hieraciodes sahendi O. Kuntze, Gen. 1: 346. 1891.

E. Turkey, Armenia, and N.W. Persia, high montane. In addition to the localities cited below, it has been reported from Mt. Alagös in W. Armenia as *Pterotheca runcinata* Trautv., *loc. cit.*, and from Mt. Meleto in the Armenian Taurus, E. Turkey, by Handel-Mazzetti (Ann. Naturhist. Hofmus. Wien 27: 458, 1913).

Monomorphic.

Persia: Aderbeidschan Prov., Sahend Mts., Schah-Jordi, 2545 m, *Buhse* in 1847 (Bo) type. **Nachitschevan Republic:** Mt. Ketshal-dagh, 2700–3000 m, on rocks, *Prilipko and Isaev* in 1934 (NY). **Armenia:** Darologu, Alagu, and near Saganachiekh, *Kariasin* in 1931 (K). **Turkey:** Erzerum, *Huet du Pavillon* in 1853 (Bo) type of *C. Huetti* Boiss.; Bitlis reg., about midway between Erzerum and Musch, steep summit of Bingöl-Dagh, in clay, 2727 m, *Kotschy* 500 in 1859 (Bo, Ucf, B, K), as *C. Huetti* Boiss.

Relationship

Crepis sahendi is closest, perhaps, to *C. connexa*; at least it stands next in degree of primitiveness, as indicated by the strong, woody, almost suffrutescent caudex, the large uniform achenes, and the relatively large corolla, anther tube, and appendages. But it is not closely related to any species in this section. In some respects it is reminiscent of *C. macropus* of W. Turkey.

127. *Crepis purpurea* (Willd.) M. Bieb.

Fl. Taur. Cauc. 2: 255. 1808. (Fig. 187.)

Perennial, 1–4 dm high; caudex 1–2 cm long, 0.5–2 cm wide, bearing scars or bases of old leaves, leafy at crown, prolonged into a strong woody oblique or horizontal subterranean stem; caudical leaves numerous, somewhat fleshy, canescent-tomentulose, 3–9 cm long, 1.5–3 cm wide, oblanceolate, acute, deeply runcinate-pinnatifid, with the segments all acutely dentate, to bipinnately divided and the secondary lobes dentate, lobes and teeth corneous-mucronate, attenuate into a narrowly winged petiole, scarious or purplish toward the broader base; cauline leaves mostly reduced to small bracts, in occasional robust specimens the lowest one or two similar to the caudical leaves; stems 1–4, erect, slender, terete, striate, puberulent or glabrous, cymosely 1–3-furcate at summit, 2–6-headed, rarely branched from near the middle, the branches 1–2-headed; peduncles 1.5–7 cm long, strictly arcuate, slender, glabrous or \pm tomentulose; heads erect, medium, many-flowered; involucre cylindric-campanulate, 10–12 mm long, 5–6 mm wide at middle in fruit, canescent-tomentose, rarely (cf. m.v. 1) pubescent with short and long yellow gland hairs; outer bracts

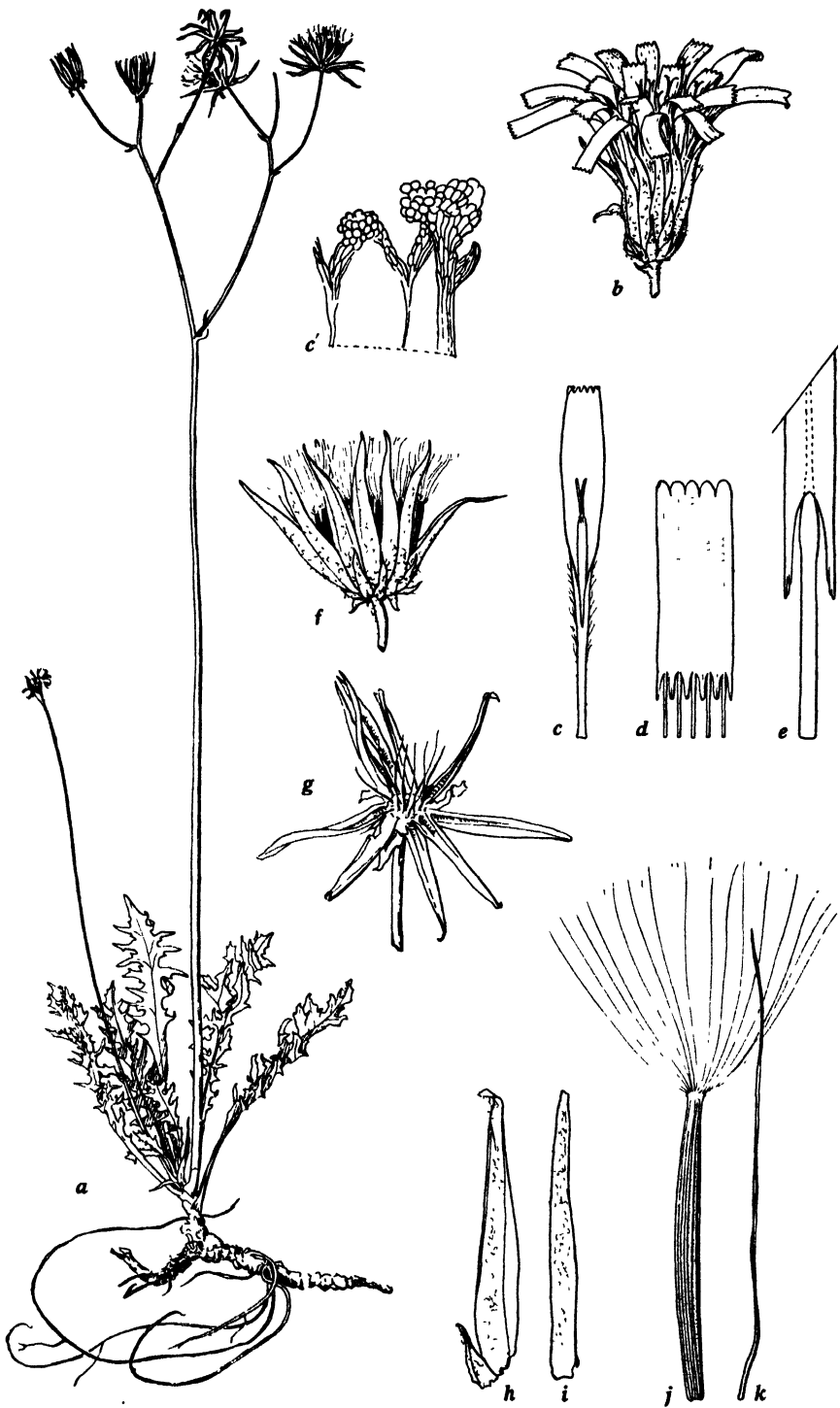


Fig. 187. *Crepis purpurea*, from Fauché in 1840 (Bo): a, plant, $\times \frac{1}{2}$; b, flowering head, $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule teeth, $\times 50$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, fruiting head, $\times 2$; g, old head, $\times 2$; h, i, inner involucre bracts, outer face, $\times 4$; j, k, achene with pappus, and a palea, $\times 8$.

10–14, imbricate, very unequal, the longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner in fruit, ovate-lanceolate to lanceolate, acute; inner bracts 13–15, lanceolate, acute, scarious-margined, glabrous within, becoming strongly carinate dorsally and spongy-thickened in fruit, ultimately reflexed; receptacle flat, paleaceous, paleae setiform, sometimes exceeding the pappus; corolla 11–12 mm long; ligule 1.5 mm wide; teeth 0.2–0.3 mm long, elaborately gland-crested; corolla tube 3.5–4 mm long, densely pubescent with strong straight several-celled trichomes 0.5–1 mm long; anther tube yellow, 3.75×1.25 mm dis.; appendages 0.45 mm long, linear, acute, united; filaments 0.6 mm longer; style branches about 1 mm long, 0.1 mm wide, obtuse at tip, green; achenes uniform, dark brown or occasionally with white sterile ones present, 4.5–5 mm long, 0.5–0.6 mm wide, columnar, curved or straight, \pm attenuate to the summit, with scarcely expanded pale pappus disk, slightly constricted at the thinly calloused hollow base, 10-ribbed, ribs rather prominent, rounded, muriculate; pappus white, about 4 mm long, 3–4-seriate, rather fine, soft, persistent. Flowering June–July; flowers bluish-purple!

Hieracium purpureum Willd., Sp. Pl. 3: 1560. 1803.

Crepis purpurea M.B., Fl. Taur. Cauc. 2: 255. 1808.

Lagoseris crepoides M.B., Cent. Fl. Bar. Ross. 1, t. 30. 1810.

L. taurica M.B., Fl. Taur. Cauc. Suppl. 539. 1819.

Intybellia rosea Cass., Bull. Soc. Philom. 124. 1821.

Myoseris purpurea Link, Enum. Alt. 2: 291. 1822.

I. purpurea DC., Prod. 7: 180. 1838.

I. purpurea Steven apud DC., loc. cit., et Boiss., Fl. Orient. 3: 883. 1875.

Pterotheca purpurea Trautv., Acta Hort. Petrop. 4: 386. 1876.

Crimea, around Karassubazar, hills or mountain slopes, on chalk deposits, said to be a cretaceous formation. No locality is cited in the original description; but Marschall-Bieberstein, in his earliest description, cites Karassubazar and mentions cretaceous rocks, but without citing any specimens. Since all the known localities are in Crimea, it appears that this species is endemic; and one collector (Zyrina, see below) states that it is endemic. Making due allowance for variations in size, the specimens seen by me are very uniform, except m.v. 1, which differs mainly in pubescence of the involucre and length of the pappus. In lieu of an authentic specimen of Willdenow or Bieberstein, the first specimen cited below is accepted as typical.

U. S. S. R.: Crimea, Karassubazar, hills, *Rehmann* in 1874 (Bo, B); *ibid.*, without locality, *Fauché* in 1840 (Bo, Ucf); *ibid.*, on chalky rocks, *Callier* in 1895 (B); *ibid.*, cretaceous rocks, *Callier* in 1896 (Bo, B); *ibid.*, Akkaja, cretaceous mountain slopes, *Callier* in 1900 (K); near the village Ak-kaja, *Zyrina* in 1926 (K) m.v. 1; Crimea, Yalta, *Zelenetzny* in 1886 (Bo).

Minor Variant of *C. purpurea*

1. Involucre and upper part of peduncle densely pubescent with short and long yellow gland hairs or setules; pappus about 5 mm long, finer and softer than in the typical form. In addition to the specimen cited below, it should be noted that three other specimens without definite locality were found to have more or less gland-pubescence on the involucre. From these data it cannot be determined whether m.v. 1 is a strictly local race or whether this variation appears here and there over the area of distribution. The latter, however, seems most likely, since one of these pubescent specimens is a fragment of inflorescence in the otherwise typical collection of *Fauché* in Herb. Boiss. *Zyrina* in 1926 (K), near the village Ak-kaja, Crimea.

Relationship

Crepis purpurea, on account of its flower color, is unique in this genus. Its strong perennial base, broad imbricate outer bracts, fairly strong ribs on the achenes and persistent pappus indicate that it is a rather primitive species; but in floral characters and habit it is more advanced than *C. sahendi*.

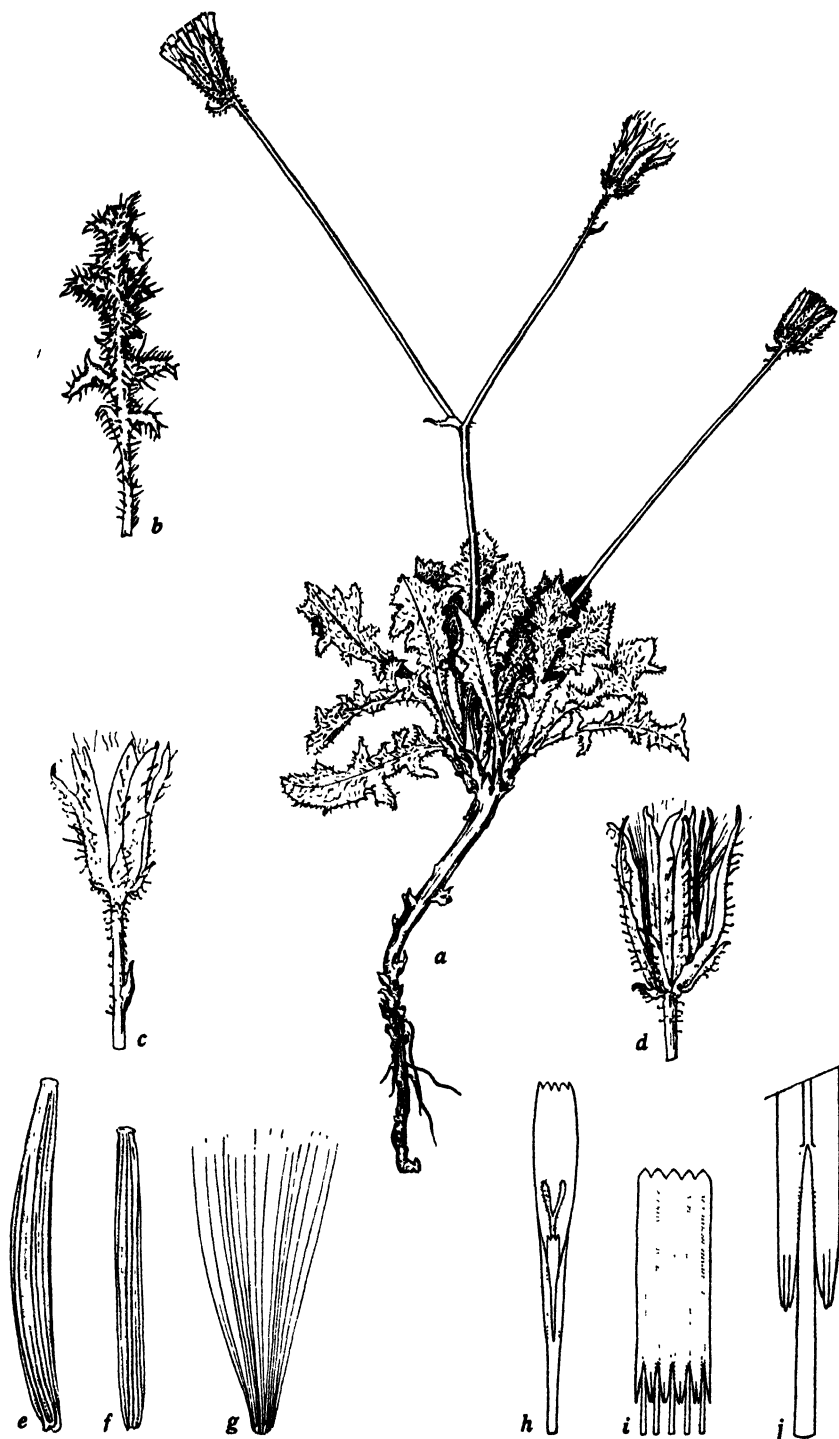


Fig. 188. *Crepis elbrusensis*, *a-c*, from Kotschy 471 (Bo); *d-g*, from Kotschy 676 (Bo); *h-j*, from Aucher 4855 (Bo): *a*, plant, $\times 1$; *b*, rosette leaf, $\times 2$; *c*, immature head showing paleae protruding beyond pappus, $\times 2$; *d*, fruiting head, $\times 2$; *e*, *f*, outer and inner achenes, and *g*, pappus, $\times 8$; *h*, floret lacking ovary, $\times 4$; *i*, anther tube, $\times 8$; *j*, detail of appendages, $\times 32$.

128. *Crepis elbrusensis* Boiss.

Diag. Pl. Or. Nov. ser. 1, 11: 58. 1849. (Fig. 188.)

Perennial, 0.6–2.6 dm high; caudex subterranean, 4–6 cm long, 1–2 mm wide, vertical or curved below, bearing several abortive leaves with vegetative buds in the axils and fine fibers near base, simple or 2–3-branched at summit, each branch bearing a dense rosette of small leaves; rosette leaves 2–4(8) cm long, 0.5–1.5 cm wide, densely pubescent with white glandless setules, oblanceolate, obtuse, mucronate at apex, lyrate-pinnately parted, terminal segment ovate to lanceolate, dentate, lateral segments oblong or triangular, gradually attenuate into a broadly winged petiole, broader and scarious at base; cauline leaves much reduced or bract-like; stems 1–3, erect, slender, terete, striate, sparsely setuliferous, 2-furcate, branches divaricate, pendunculate; peduncles pubescent with very short gland hairs, \pm tomentose near head; heads erect, medium, 20–30-flowered; involucre cylindric-campanulate, 9–11 mm long, 5 mm wide in fruit, gland-pubescent at base, canescent-tomentose, \pm setuliferous, setules mostly pale and glandless; outer bracts 8, unequal, longest about $\frac{1}{3}$ as long as inner bracts, lanceolate, acute, with narrow pale scarious band at margin; inner bracts 10–13, lanceolate, acute or acuminate, with broad pale scarious band at margin, becoming dorsally carinate and spongy-thickened near base, sparsely pubescent or glabrous on inner face; receptacle paleaceous, paleae pale brown, setiform, slender, up to 12 mm long, simple or furcate at apex, equal to or exceeding the pappus; corolla 10–12 mm long; ligule 1.4 mm wide; teeth 0.15–0.25 mm long; corolla tube 2.5–3 mm long, pubescent with very short acicular hairs (0.08–0.3 mm long); anther tube 3.6×1.2 mm dis.; appendages 0.6 mm long, lanceolate, acuminate; filaments 0.5 mm longer; style branches 1.25–1.5 mm long, 0.1 mm wide at base, gradually increasing to 0.15 mm wide at tip, obtuse, yellow; achenes essentially uniform, all stramineous, terete or subterete, equally attenuate to summit and base, with slightly expanded pappus disk and lightly calloused base, 15–17-ribbed, ribs all narrow but somewhat unequal, rounded, glabrous, marginal achenes larger, 5.5 mm long, 0.5–0.6 mm wide, somewhat curved, inner achenes 4.75 mm long, 0.4–0.5 mm wide, straight; pappus white, 5 mm long, equal to involucre in fruit, 2–3-seriate, very fine, soft, united at base, falling away in a ring, caducous. Flowering July–Aug.; flowers yellow.

Hieraciodes elbrusense O. Kuntze, Gen. 1: 346. 1891.

N. Persia, in the W. part of the Elburz Mts., and on Mt. Totschal near Teheran. The type locality is a place called Char Gerdene, near the village Asadbar. The locality cited below for Aucher's spec. is unknown to the present writer, but it is cited by Boissier as though it were in the type reg., the W. Elburz Mts.

Monomorphic.

Persia: W. Elburz Mts., near the village Asadbar, "Char Gerdene," *Kotschy* 471 (type Bo, K, B, Mo); "Elamont" (= Mt. Elamont), *Aucher* 4855 (Bo, UCf)§ near Teheran, Mt. Totschal, Barenginon Peak, 2440 m, *Kotschy* 676 (Bo, Mo, UCf).

Relationship

Crepis elbrusensis is probably closest to *C. frigida*, which is very different in its inflorescence, the heads being borne on very short scapes, also in shape of leaves, in the tomentum on leaves, peduncles, and involucre, and in the broader achenes.

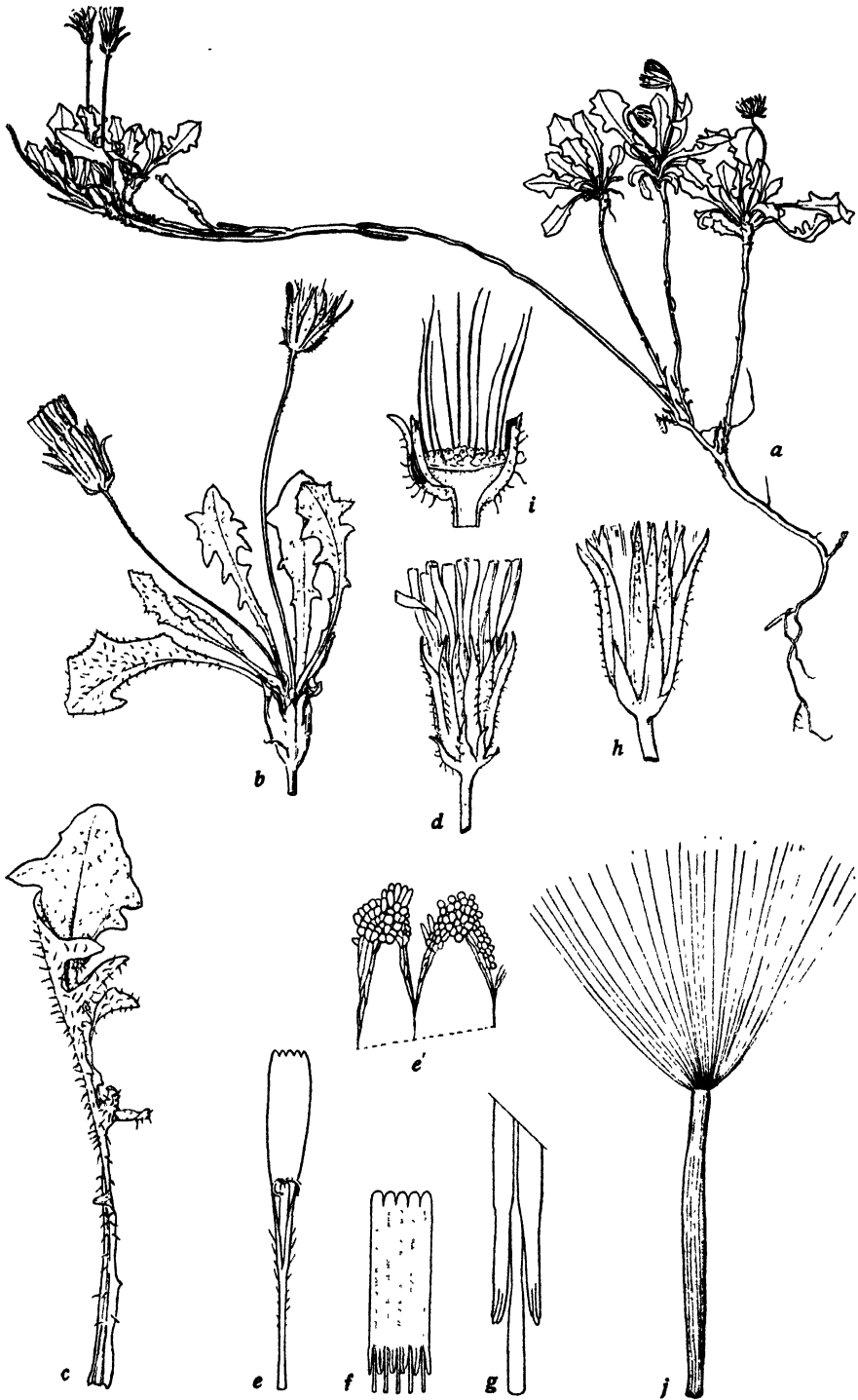


Fig. 189. *Crepis frigida*, from type (Bo): a, plant, $\times \frac{1}{2}$; b, plant, $\times 1$; c, leaf, lower and upper faces, $\times 2$; d, flowering head, $\times 2$; e, floret lacking ovary, $\times 4$; e', detail of ligule teeth, $\times 50$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, fruiting head, $\times 2$; i, part of receptacle, with paleae, $\times 4$; j, achene, $\times 8$.

129. *Crepis frigida* (Boiss.) comb. nov.

(Fig. 189.)

Perennial, with small rosettes and scapelike stems, 0.3–0.6 dm high, borne on long slender shoots arising from buds on a subterranean caudex; caudex slender, woody, leafy at crown; caudical leaves rosulate, up to 3.5 cm long, 1.5 cm wide, petiolate, oblanceolate to spatulate, obtuse or acute, denticulate to lyrate-pinnatifid with 3–4 pairs of small oblong lateral lobes, densely canescent-tomentose on upper face, densely pubescent notably on lower face with yellow hairs or setules; stems pedunculate, slender, terete, tomentulose, \pm gland-pubescent; heads erect, medium, many-flowered; involucre cylindric-campanulate, 9–12 mm long, 3–5 mm wide at middle in fruit, canescent-tomentose; outer bracts 7–9, unequal, longest $\frac{1}{3}$ – $\frac{2}{3}$ as long as the inner, lanceolate, acute; inner bracts 12–16, lanceolate, acuminate, dorsally pubescent with glandular or glandless setules, ventrally glabrous, scarious-margined, rounded-carinate dorsally and obscurely spongy-thickened at base in fruit; receptacle flat, paleaceous with setiform paleae longer than the achenes, not exceeding the pappus; corolla about 12 mm long; ligule 1.5 mm wide; teeth 0.25 mm long; corolla tube about 4 mm long, pubescent with coarse straight several-celled trichomes 0.7 mm long; anther tube 3×1 mm dis.; appendages 0.5 mm long, narrow, obtuse; filaments 0.3 mm longer; style branches yellow, about 1 mm long, narrow, obtuse at tip; achenes light brown, about 5 mm long, uniform, columnar or curved, subterete, slightly attenuate upward, with small pale pappus disk, narrowed at the lightly calloused base, 15-ribbed, ribs close, rounded, smooth; pappus white, about 4 mm long, 3-seriate, rather fine, soft, deciduous in clumps. Flowering July–August; flowers yellow.

Derouetia frigida Boiss. et Bal., Diag. Pl. Or. Nov. ser. 2, 5: 114. 1856.

Lagoseris frigida Boiss., Fl. Orient. 3: 882. 1875.

D. Robertioides Boiss., *D. Bourgaei* Boiss., and *Intybellia glareosa* Schott et Ky., ex Boiss. loc. cit.

Pterotheca glareosa Trautv., Act. Hort. Petrop. 4: 386. 1876.

Central Turkey, in the Masmeneudagh and Argaeus (Ercis) Mts., at 2700–3200 m alt., alpine zone, on loose rocks; S. Turkey in the Taurus Mts., at about 2200 m alt., gravelly slopes of Mt. Koschan; and S.W. Turkey in the Lycian Taurus, Mt. Ak-Dagh.

Turkey: Cappadocia, summit of Masmeneu-Dagh, 3200 m, situated 100 kilometers to the southwest of Césarée (Kasarié), *Balansa* 1024 in 1855 (Bo type, K, G, UCf); Cappadocia, Mt. Argaeus (Ercis) alpine reg., *Balansa* 780 in 1856 (Bo); Cilicia, Taurus, Bulgar Daghl, Mt. Koschan, *Kotschy* in 1853 (Bo); Lycia, Mt. Ak-Dagh, alpine reg., in gravel, *Bourgeau* in 1860 (Bo, K) m.v. 1.

Minor Variant of C. elbrusensis

1. (*Lagoseris frigida* var. *Bourgaei* Boiss., loc. cit.) The leaves are not tomentose and are more densely pubescent on the upper than on the lower face; stems 0.3–0.8 dm high; heads rather variable in size, the involucre 4–6 mm wide at middle or more, and in the plants with larger heads the involucre bracts are notably wider. *Bourgeau* in 1860 (Bo, K) as *Derouetia Bourgaei* Boiss., alpine reg., in gravel, Mt. Ak-Dagh, Lycia, S.W. Turkey.

Relationship

Crepis frigida is apparently nearest to *C. elbrusensis*, but the two species differ in many characters, notably in the inflorescence, in the indumentum of the leaves, and in various details of flowers and fruits.

SECTION 17. NAPISERIS

130. *Crepis napifera* (Franch.) comb. nov.

(Fig. 190.)

Perennial, 4–15 dm high; root narrowly napiform or columnar, prolonged downward into a strong taproot, often constricted below the simple or divided summit; caudex 1–2.5 cm long, 0.5–1.5 cm wide, covered with brown bases of old leaves and with \pm brown wool, leafy at summit; caudical leaves 7–26 cm long, 2.5–6.5 cm wide, elliptic to oblanceolate, short- or long-petiolate, obtuse or rarely acute, denticulate, repand to coarsely runcinate or shallowly lobed with a few broad triangular or rounded segments, pubescent on both sides with short glandless hairs; lowest cauline leaves similar but reduced, the others small, linear or bractlike; stem erect, 2–5 mm wide at base, terete, striate, glabrous below, puberulent above, closely branched toward summit, branches very short, bearing 1–8 heads in a congested cluster, aggregate inflorescence paniculate-racemiform; peduncles 2–5 mm long, bracteate; heads erect, rather small, 5–10-flowered; involucre 7–9 mm long, cylindric, pale or dark green, glabrous; outer bracts 6–8, unequal, longest $\frac{1}{4}$ – $\frac{1}{2}$ as long as inner bracts, lanceolate, acute, ciliate on margin or at tip, like inner bracts mediodorsally nerved, the nerve thickened or tuberculate near tip; inner bracts 5 or rarely 6, linear-lanceolate, obtuse, ciliate at tip, glabrous on inner face; receptacle areolate, naked; corolla about 11 mm long; ligule 2 mm wide; teeth 0.25–0.4 mm long; corolla tube 3.5–4 mm long, sparsely pubescent with stout several-celled sometimes branching trichomes up to 0.1 mm long; anther tube 3.6×1.1 mm dis.; appendages 0.5 mm long, oblong, truncate; filaments unequal, 0.75–1.1 mm longer; style branches brown in sic., 1.25 mm long, 0.1 mm wide at base, 0.15 mm wide near the apex, acute; achenes light or dark brown, 3.5–4.5 mm long, about 0.5 mm wide, straight or curved, subterete or obscurely angled, gradually attenuate upward, with expanded pappus disk, constricted at the calloused base, 10-ribbed, ribs nearly equal in width or with 2–5 wider, obscurely spiculate; pappus yellow, about 4 mm long, 1-seriate, somewhat unequal, rather stiff and brittle, persistent. Flowering Aug.–Oct.; flowers yellow.

Lactuca napifera Franchet, Jour. Bot. 60: 292–293. 1895.

Prenanthes Chaffanjonii Lévillé, in Fedde, Repert. 11: 305. 1912.

S.W. China and S.E. Tibet, at elevations ranging from 1400 to 3300 meters, in pine and scrub oak forests and on open grassy or rocky plains. The range of the species is comparable to that of *C. Phoenix*, *C. Bodinieri* and *C. rigescens* subsp. *typica* combined (see fig. 191, areas 1, 2, 3a).

Monomorphic.

China: Yunnan, pinewoods near Ta-pintze, *Delavay 574* (P, UCf) type or isotype; Yunnan, Mongtaze, *Henry 9952A* (US, UCf); Yunnan, *Maire* (UC); Yunnan, Wei-se Hsien, 2800 m, forest, *Tsai 59565* (G, UC); Yunnan, Chih-tse-lo, ravine, 2500 m, *Tsai 54165* (G, UC); Yunnan, Lan-ping Hsien, ravine, 2500 m, *Tsai 56215* (G, UC); Yunnan (?), Honang-tsao-pa, *Cavalerie 4061* (G); Yunnan, E. base of Snow Mts., near Lichiang, *Schneider 3016* (G); N.W. Yunnan, E. slopes of Likiang Snow Range, open scrub forest, 3000 m, *Rock 5822* (US, NY, UCf); *ibid.*, Sa Ba, 3300 m, *Rock 5661* (US); Kweichow, around Kweiyang, "Mont. du Collège," *Chaffanjon 2468* (E) as *Prenanthes Chaffanjonii* Lév.; Kweichow, "route de Pe-gai-yu," *Esquirol 2728* (E, UCf)), as *P. Chaffanjonii* Lév.; S.W. Szechuan, between Yalung and Nganningho rivers, near Puti, 27° 4' N., among pines, 1400–1700 m, subtropical, *Handel-Mazzetti 5273* (MW); *ibid.*, Yenyüen, grassy, stony plain, 2700–2800 m, cold-temperate, *Handel-Mazzetti 5467* (MW, UCf). **Tibet:** Mekong-Salween divide, Mt. Dokerla, 28° 20' N., dry open pine forest, 2100–2700 m, *Forrest 14869* (MW).

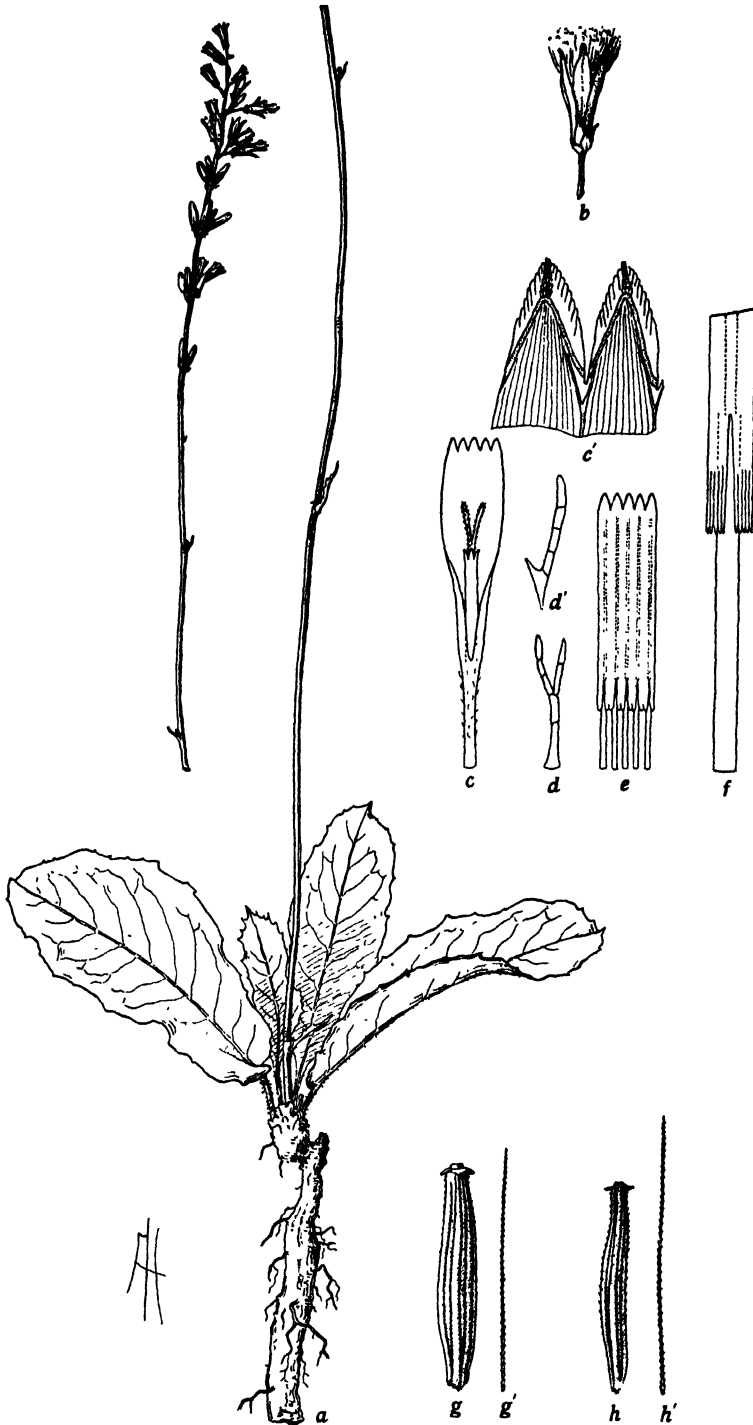


Fig. 190. *Crepis napifera*, a, b, from Delavay 574 (P) type or isotype; c-f, from Handel-Mazzetti 5467 (MW); g, g', from Chaffanjon 2468 (E); h, h', from Henry 9952A (US): a, plant, $\times \frac{1}{2}$; b, fruiting head (immature), $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule teeth, $\times 50$; d, d', trichomes of corolla tube, $\times 100$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, g', achene and pappus seta, $\times 8$; h, h', achene and pappus seta, $\times 8$.

Relationship

The classification of this species in *Lactuca* by Franchet probably resulted from his conviction, based on the intergradation between *Lactuca* and *Prenanthes* which he observed in certain Asiatic species, that these two genera should be merged. Franchet's statement that this species resembles *Prenanthes virgata* Mich. of E. North America is based mainly on superficial similarity in habit. In *P. virgata* the caudical leaves are deeply pinnatifid, the stem, though scapiform, is conspicuously leafy, and the involucre, florets, and achenes are all typical of *Prenanthes*. A much better choice for comparison with *Prenanthes* would have been either *P. sinensis* (Hemsl.) Stebbins ined. (*Fabertia sinensis* Hemsl., Jour. Linn. Soc. 23: 479. 1888) or *P. Ceterach* (Beauverd) Stebbins ined. (*F. Ceterach* Beauverd, Bull. Soc. Bot. Genève, Ser. II, 2: 251. 1910), in which the caudical leaves resemble those of *C. napifera* and the scapiform stem is nearly naked. But in these species the inflorescence is paniculate and the involucre, flowers, and fruits are all typical of *Prenanthes*.

But these anomalous species which show affinities with more than one Cichorieaceous genus are few in number and they all occur in E. Asia. Several occur only in the Himalaya Mts. and adjacent areas. This region became an important secondary center of geographic distribution in the Cichorieae. But the center of origin of the Asiatic representatives of these genera lay farther to the north in Asia. From this viewpoint the existence of such species is just what could be expected, and the fact of their existence need not in any way weaken the generally accepted delimitation of such large genera as *Lactuca*, *Prenanthes*, and *Crepis*.

C. napifera is essentially *Crepis*-like in all its characters except the racemiform inflorescence which, although rare in this genus (cf. *Youngia racemifera*, p. 925), may be considered as a contracted panicle. Although certain characters of *C. napifera* are rare in this genus, yet they are found in other species which have been assigned without question to *Crepis*. For example, the napiform root occurs in *C. subscaposa* and sometimes in *C. runcinata*; the large, fleshy, caudical leaves show considerable resemblance to those of some forms of *C. runcinata*; the tall, scapelike stem with reduced bractlike leaves is characteristic of many species of *Crepis* and the racemiform inflorescence is found in *C. praemorsa*; the small number of florets per head is much less common in this genus but is found in the diploid forms of several American species, also in *Crepis nana* and its close relatives. The peculiar, blunt, several-celled hairs on the corolla tube also occur in *Youngia setigera* (cf. p. 925). The marked tendency to have unequal ribs on the achenes, as well as the racemiform inflorescence (cf. *Y. stenoma* and *Y. racemifera*), also suggests relationship with *Youngia*. Thus, *C. napifera* may well be considered as derived from the ancestral stock of both *Crepis* and *Youngia*.

In this connection it is significant that the pollen grains of *C. napifera* bear small spines which are characteristic of *Crepis*; also that the grains are 3-pored and average 27–28 μ in diameter. The small size of the pollen grains and of the stomata, which average 33–34 μ , indicate that this species may have 4 or 5 pairs of medium-sized chromosomes, somewhat resembling the primitive karyotype of *Crepis*. Chromosomes of smaller size than those of *C. sibirica*, for instance, would be anticipated, since *C. napifera* must be considered more advanced than *C. sibirica* on account of the general reduction throughout its inflorescence. At the same time, the morphological evidence that it had a common origin with *C. praemorsa* (see p. 553) would suggest either a karyotype similar to that of the latter species or one from which the karyotype of *C. praemorsa* could have been derived.

SECTION 18. PYRIMACHOS

The 5 species in this section have a perennial woody caudex and a deeply penetrating taproot. This makes recaulescence possible, after fires have destroyed all of the plant above the soil surface, which gave both the type species, *C. Phoenix*, and the section their names. The most distinctive feature of this remarkable group, however, is found in the scalelike, persistent, lowest cauline leaves or cataphylls. The other cauline leaves are narrowly lanceolate or linear and gradually become larger, reaching maximum size near or above the mid-region, after which they are gradually reduced to mere bracts in the upper part of the inflorescence. Caudical leaves are absent in mature plants, and the juvenile state has not been observed. The stem or stems are erect, ligneous, \pm branched, the branches fastigate, strict or somewhat divaricate; the heads small to medium, 7–25-flowered; and the involucre cylindric-campanulate, with narrow outer bracts which are $\frac{1}{4}$ – $\frac{2}{3}$ as long as the inner ones, the inner bracts glabrous on inner face, becoming carinate on outer face and thickened at the base. Receptacle naked; corolla yellow, 10–15 mm long, the tube 3–4 mm long; achenes brown, fusiform, subterete or subcompressed, 10–16-ribbed, the ribs nearly equal or with several stronger ones; pappus white or cream colored, 3–6 mm long, mostly 1-seriate, the setae often unequal, persistent.

These species are all endemic in S.E. Asia, mostly in S.W. China from S.W. Kweichow and Szechuan throughout Yunnan. One species extends into N. Siam and occurs in S. Annam; and two occur in Burma. They are distributed at elevations ranging from 1000 m to 3900 m, mostly between 1500 m and 2500 m; and they are frequently found in dry pastures and on exposed slopes. The largest number of forms have been reported from Mengtze and Yunnanfu, in E. Yunnan; but this may be merely the result of more intensive collecting in those districts.

Crepis Phoenix may be considered as somewhat more primitive than the other four species on account of its larger leaves, heads, and achenes. It occurs sporadically in E. Yunnan (cf. fig. 191). *C. Bodinieri* stands next and it occurs in N. Yunnan and S. Szechuan. *C. rigescens* is intermediate between the first two species and *C. lignea*. *C. rigescens* subsp. *typica* occurs in N.W. Yunnan in an area adjacent to that of *C. Bodinieri*. *C. rigescens* subsp. *lignescens* has been collected at 2 localities in W. Yunnan and at one in W. Burma. *C. lignea* is the most widespread species, being distributed from S. Szechuan and Kweichow southward through Yunnan into N. Siam; and it has been collected twice in the Langbian Mts., in S. Annam.

This section is a transitional group between *Crepis* and *Ixeris*. At one extreme is *C. Phoenix*, in which leaf shape, habit, size of heads, and type of involucre are all positively *Crepis*-like. The achenes, however, are rather irregular in amount of compression and are somewhat unevenly ribbed. At the other extreme is *C. lignea*, in which the heads are more numerous and smaller; and the achenes show considerable resemblance to those of *Ixeris* species, although they are not so definitely beaked and the ribs are somewhat unequal. *C. Bodinieri* and *C. rigescens* are intermediate, the former being closer to *C. Phoenix*, and the latter being connected with *C. lignea* through subsp. *lignescens*. The fifth species, *C. chloroclada*, is known only from the type; but it also approaches *C. lignea*.

Pyrimachos, however, is distinct from both *Ixeris* and *Youngia*, and from all other species of *Crepis* in the peculiarity of having the lower cauline leaves reduced to cataphylls, whereas in the mid-region the cauline leaves gradually reach their maximum size and decrease again toward the top of the plant. These five species,

therefore, stand apart from all other species of *Crepis*, even from those found in the same region, whereas they exhibit some evidence of relationship, particularly in their achenes, with *Youngia* and *Ixeris*, both of which genera occur in the same general region.

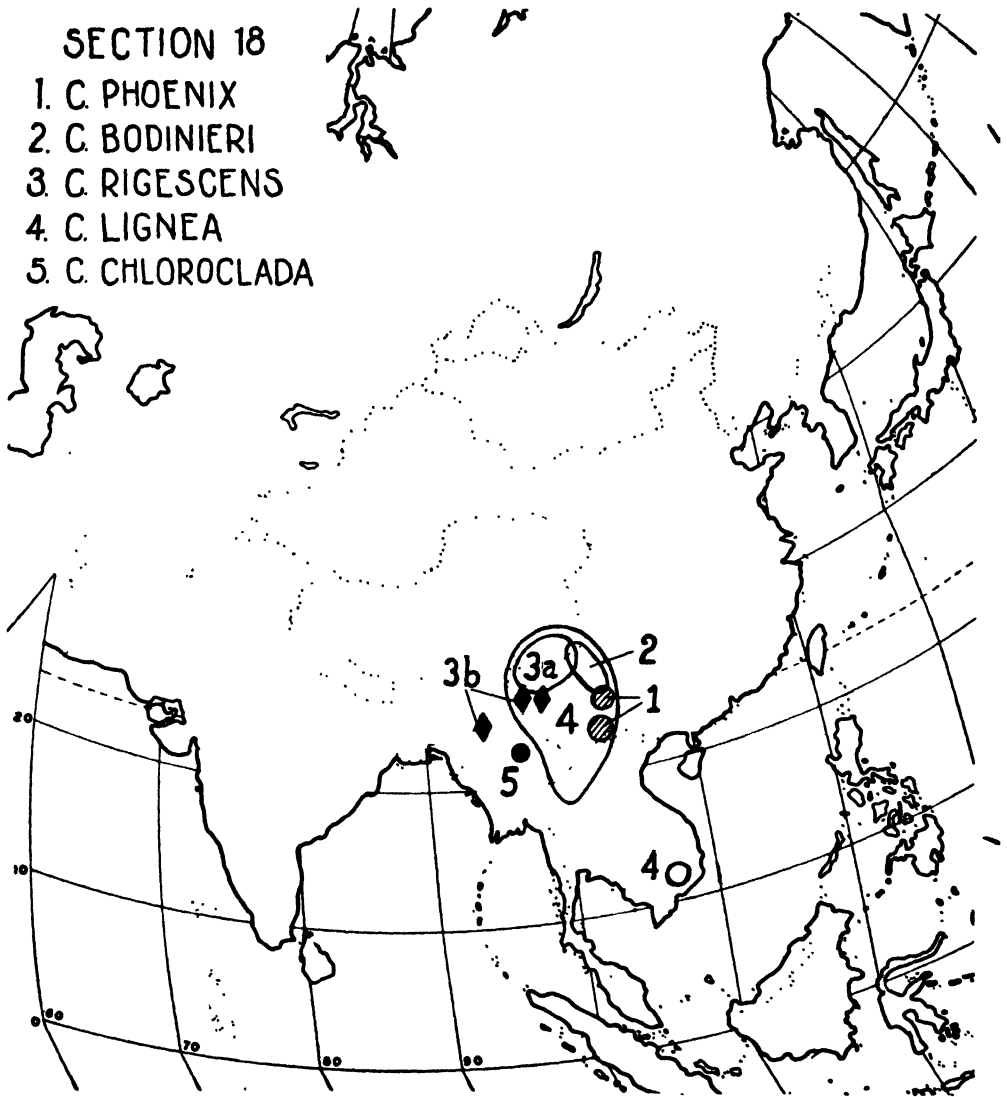


Fig. 191. Geographic distribution of the 5 species in sec. 18. Single known stations are shown by solid circles, and 3 known stations by solid diamonds. The remaining areas contain more than 4 known stations. Based on Goode *Base Map No. 201 PC*. By permission of the University of Chicago Press.

Unfortunately, no information concerning the chromosomes of these species is at present available. But an examination of the pollen grains by Stebbins (unpublished data) has provided evidence which supports their classification under *Crepis*. In all five species the size of the pollen grains and the character of the spines indicate a basic number lower than 8. The 8-chromosome species of *Ixeris* and *Youngia* have pollen grains about the same size as these species, but the spines are, as a rule,

smaller in relation to the size of the grains, which is typical of those species in the *Crepidinae* with small and relatively numerous chromosomes. The pollen grains of the members of this section, however, are not very different from those species of *Crepis* having 5, 6, and 7 as haploid numbers, and the stomatal size is comparable. Hence, basic numbers of this order are most probable, although some of the diploid forms may be 4-paired. Thus, the morphology of the pollen grains supports the conclusion drawn from the morphology of the plants that these six species belong in *Crepis*, although they show affinity with both *Youngia* and *Ixeris*. It is not improbable that they have been derived from a common ancestral stock through interspecific hybridization.

More or less irregularity of the pollen has been noted in numerous forms. Some of this may, of course, be due to environmental conditions or to genes for asynapsis, but in several of these forms the comparative morphology of the plants also suggests the occurrence of natural hybridization. Also, the existence of occasional variants with 4-pored as well as 3-pored pollen grains, along with a high degree of irregularity in the pollen, indicates that these forms are unbalanced polyploids which reproduce to some extent at least by apomixis. In fact, each of four of these species (*C. Phoenix*, *C. Bodinieri*, *C. rigescens*, and *C. lignea*) appears to be a complex of diploid and polyploid forms. Similar complexes have been found in several species of *Youngia*, e.g., *Y. paleacea*. The existence of such complexes of diploid and polyploid forms, probably including hybrids and apomicts, makes the recognition of well-defined species extremely difficult. It is even possible that adequate cytotaxonomic research on this section will reveal the necessity of a revised treatment of the group along the lines adopted for the American species of *Crepis*. Meanwhile, the following key and taxonomic disposition of the species and variants seems to be the best that can be done with our present inadequate knowledge of these plants.

Key to the Species of Section 18

- Leaves flaccid, setose or setulose on lower face or canescent-tomentulose on upper face; involucre 3-4 mm wide at receptacle; heads 18-27-flowered.
 - Leaves 3-25 mm wide; leaves and involucre setose or setulose; achenes 10-ribbed.....131. *C. Phoenix*, p. 635
 - Leaves 1.5-8 mm wide; leaves and involucre canescent-tomentulose; achenes 14-ribbed.....132. *C. Bodinieri*, p. 638
- Leaves coriaceous, glabrous on both sides or tomentulose on lower face; involucre 1.5-2.5 mm wide at receptacle, or if 2-4 mm wide (*C. rigescens*, m.v. 1-4), then the leaves narrow, coriaceous, glabrous; heads 7-12-flowered (15-23-flowered in *C. rigescens typica*, m.v. 3 and 4).
 - Stem branched above or near the middle, the branches divaricate; cauline leaves up to 6-10 cm long, 3-4 mm wide; inner involucre bracts lance-linear, acuminate.....133, a. *C. rigescens*, subsp. *typica*, p. 642
 - Stem branched from near base or below the middle, the branches fastigiata or strict; cauline leaves up to 2.5-4 or sometimes 7 cm long, 1-2 (or 3) mm wide; inner involucre bracts lanceolate, mostly obtuse.
 - Involucre 7-9 mm long, 1.5-2.5 mm wide at receptacle; outer bracts unequal, the longest $\frac{1}{4}$ - $\frac{1}{2}$ as long as the inner bracts; inner bracts becoming spongy-thickened near base in fruit, the gland hairs unchanged; style branches 1-1.75 mm long.
 - Inflorescence congested, many-headed; largest cauline leaves not more than 3 cm long, less than 1 mm wide, filiform or subulate; anther tube 3.5 mm long; style branches about 1 mm long.....134. *C. lignea*, p. 644
 - Inflorescence open, few-headed; largest cauline leaves up to 4 or 5 cm long, 2 mm wide, linear; anther tube 4.5 mm long; style branches 1.75 mm long.....133, b. *C. rigescens*, subsp. *lignescens*, p. 643

Involucre 6–7 mm long, 1–2 mm wide at receptacle; outer bracts nearly equal, about $\frac{1}{2}$ as long as the inner bracts; inner bracts becoming strongly carinate and coriaceous, the gland hairs becoming setiform, in fruit; style branches less than 1 mm long.....135. *C. chloroclada*, p. 647

131. *Crepis Phoenix* Dunn

Jour. Linn. Soc. 35: 511. 1903. (Fig. 192.)

Perennial, 1.5–7 dm high; caudex vertical, slender, woody, indurate, simple or 2–3-branched at summit, leafless; stem erect, sinuate, terete, sulcate or angled, woody, green, glabrous near base, \pm setose toward summit, the setae pale, eglandular and purple-tipped, \pm branched, the branches remote, leafy, 1–7-headed, setose or glabrate; cauline leaves gradually increasing in size from base to middle of stem or higher and then decreasing upward, lower leaves 0.5–2 cm long, triangular, acute, sessile, subamplexicaul, middle leaves 2–8 cm long on different plants, 3–25 mm wide, lanceolate, acute, sessile, attenuate or rounded and subamplexicaul at base, denticulate, margins narrowly retrorsely revolute, prominently veined, glabrous, setulose or densely setose, uppermost leaves bractlike; peduncles 0.5–3.5 mm long, setulose or glabrous, tomentulose near head; heads erect, medium, 22–25-flowered; involucre 8–11 mm high, 3–3.5 mm wide at receptacle, becoming lax in fruit, canescent- or pale fuscous-tomentose, setose; outer bracts 8, unequal, longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as inner bracts, linear or subulate, obtuse or acute; inner bracts 12–14, lanceolate, obtuse, ciliate at tip, innermost broadly scarious-margined, ventrally glabrous, dorsally setulose to strongly setose along median nerve especially toward tip and sometimes crested with a green setiform claw, becoming carinate and pale, spongy-thickened toward base in fruit; receptacle glabrous; corolla 13 mm long; ligule 1.75–2 mm wide; teeth 0.3–0.6 mm long; corolla tube 3.75–4 mm long, prominently veined, glabrous; anther tube (3.5)5 \times 1(1.25) mm dis.; appendages 0.7–1 mm long, oblong, acute or acuminate; filaments 0.7 longer; style branches 1.1–1.6 mm long, 0.1 mm wide; achenes brown, 4–5 mm long, 0.5 mm wide, ventrally straight, dorsally convex, irregularly subcompressed or subterete, fusiform, gradually attenuate to summit, with expanded pappus disk, constricted at the pale-calloused hollow base, about 10-ribbed, alternate ribs sometimes narrower, finely spiculate, spicules yellow; pappus white or pale cream colored, 5.5–6.5 mm long, 1-seriate, rather coarse, somewhat brittle, persistent. Flowering Feb.–June; ligules, anthers, and style branches yellow.

S.W. China, in E. Yunnan, mountain pastures, waste places, and dry exposed slopes, from 1500 to 2000 m. Apparently not common but sporadic and local, although very few collections have been made and the field notes are very meager. Dunn (*loc. cit.*), noting the charred ends of old stalks, inferred that this species occurs in areas subject to fires and that the plants sprout again from the woody base. Similar evidence has been found by the present author concerning other species of this section.

This species is evidently a complex of diploid and polyploid or possibly hybrid forms, some of which may be apomictic. Not only is there considerable variation in size of plant, leaves, and heads, but a study of the pollen shows significant differences (see minor variants). The scanty material at present available, however, is hardly sufficient to warrant the recognition of subspecific entities other than forms, especially in view of the fact that all but one of the specimens before the writer at the present moment are from one locality, i.e., Mengtsze. The specimens of Maire from Yunnansen and of Ducloux from Yunnanfu have been seen, but in only one of them has the pollen been examined (cf. m.v. 6). Among the Mengtsze plants there are at least 5 forms which differ more or less from the type, as noted below

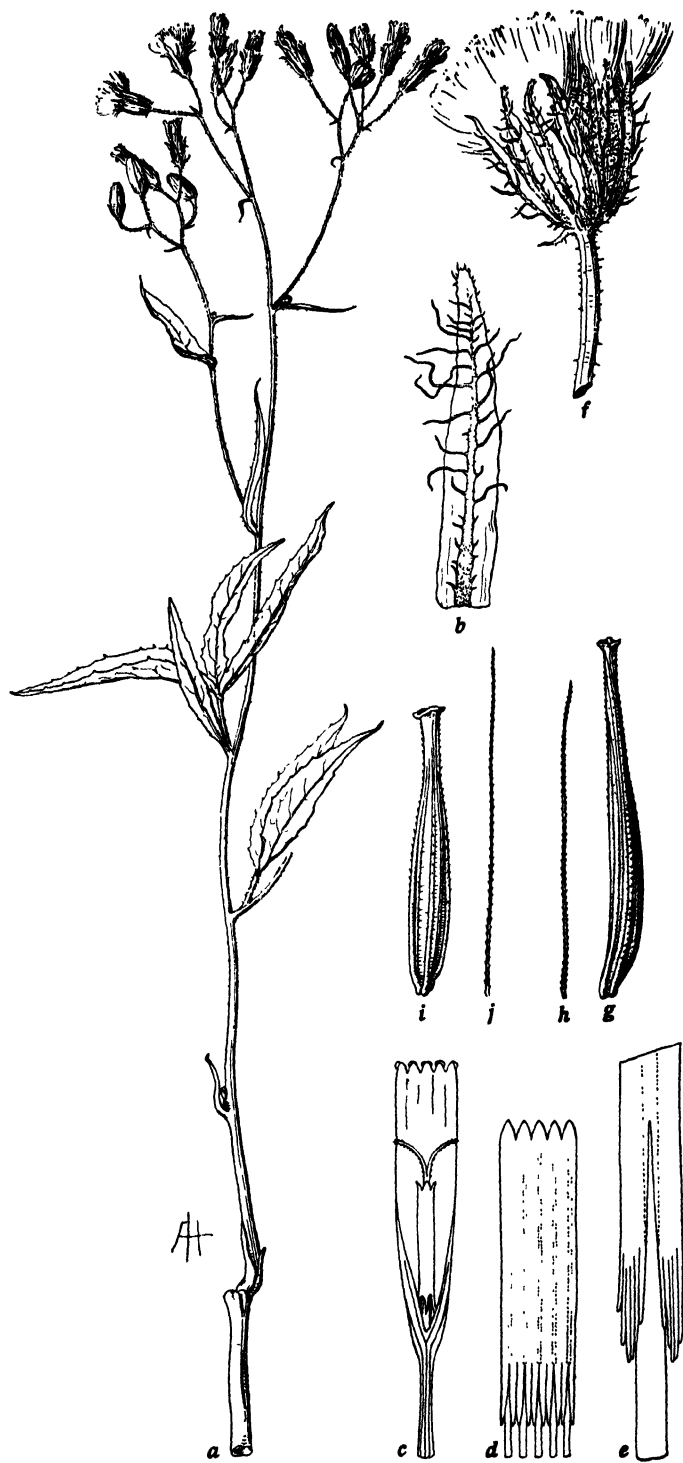


Fig. 192. *Crepis Phoenix*, a, b, from m.v. 1 (K); c-h, from *Henry 10290A* (K); i, j, from *Henry 10290D* (US 457745): a, plant, $\times \frac{1}{2}$; b, inner involucre bract, $\times 4$; c, floret lacking ovary, $\times 4$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, fruiting head, $\times 2$; g, h, achene and pappus seta, $\times 8$; i, j, achene and pappus seta, $\times 8$. Checked with material from the type, c, d, e were found to be practically identical.

under numbered variants. Four of these (m.v. 2–5) are found among the collections of A. Henry under number 10290 (K, US, NY) and, although these plants were given the same number, the original labels show that they were collected at different stations. But since the master label gives Mengtsze as the locality of each, it may be inferred that the actual stations are all in the vicinity of Mengtsze. Since the original description is based on three of these different forms, one of the three has been accepted as the type specimen. This plant (*Hancock 162B*) has smaller leaves and heads than *162A* (m.v. 1), which is on this same sheet and is the plant shown in fig. 192, *a*. The type has regular, 3-pored pollen grains, averaging $29\text{--}30\mu$ in diameter, from which it may be inferred that it is a diploid. In the type the plant is 3.5 dm high, and the largest cauline leaves are only 3 cm long and 4 mm wide; the involucre is 9 mm high; anthers 3.5 mm long; style branches 1.1 mm long. The other floral measurements agree with those of m.v. 1. There are no achenes on the type.

Yunnan: Mengtsze, mountain pastures and waste places, local, *Hancock 162B* (K, UCf) type; *ibid.*, *Hancock 162A* (K) m.v. 1; Mengtsze, grass mts., *Henry 10290A* (K, UCf) m.v. 2; Mengtsze, road hill, Feb. 20, *Henry 10290B* (NY) m.v. 3; Mengtsze, solitary pine mt., May 9, *Henry 10290C* (NY) m.v. 4; Mengtsze, Apr. 9, *Henry 10290D* (US, UCf) m.v. 5; Mengtsze, June 20, *Henry 10290E* (US) m.v. 2; Yunnanfu, *Ducloux 293* (K); Yunnansen, *Maire 1569, 1570* (K) m.v. (?); *ibid.*, *Maire 1570* (UC) m.v. 6.

Minor Variants of *C. Phoenix*

1. Cauline leaves up to 5 cm long, 5 mm wide, narrowly rounded at base; involucre 11 mm high, 3.5 mm wide; anther tube about 4.5 mm long. The pollen grains are 3-pored but irregular in size and sculpturing, $30\text{--}37\mu$ in diameter, averaging 33μ . It is probable, therefore, that this is an unbalanced polyploid and, since the partly mature heads are well filled with achenes, it may be an apomict. *Hancock 162A* (K) Mengtsze, Yunnan.

2. Plant only 1.5–2 dm high; cauline leaves up to 6 cm long, 1.5 cm wide, broadly rounded at base, subamplexicaul; involucre 10–11 mm long, 2.5–3 mm wide; anther tube 5 mm long. The pollen grains are irregular, somewhat as in m.v. 1, but there are plenty of well-developed achenes, which indicates that this is also an apomictic polyploid. *Henry 10290A* (K), grass mts., Mengtsze, Yunnan.

3. Plant 7 dm high; cauline leaves up to 6 cm long, 1.3 cm wide, *narrowly elliptic, equally attenuate at base and apex*; involucre about 10 mm high; corolla 13 mm long; ligule 2 mm wide; teeth 2.5–5 mm long; corolla tube 3.5 mm long, glabrous; anther tube 4.6×1.2 dis.; *appendages 0.5 mm long, oblong, obtuse, united*; *filaments short*, only 0.4 mm longer; style branches 1.6 mm long, 0.1 mm wide; achenes lacking; pappus cream-white, about 6 mm long, 1-seriate. Ligules, anthers, and styles yellow. On account of the definite differences between this and all the other forms, including the type, in shape of leaves, length of filaments, and length and shape of the anther appendages, the elevation of this form to the rank of subspecies would perhaps be warranted. At present, however, there is only one specimen which lacks fruits, and apparently it is merely an extreme variant in the polymorphic complex existing in the vicinity of Mengtsze. Except that the cauline leaves are larger and *not at all rounded at the base*, they resemble those of the type in which the cauline leaves are also narrow at the base and slightly rounded. The pollen grains of this variant are regular, 3-pored, and average 30μ in diameter, which may indicate that it is a diploid. For the present, however, the author prefers merely to call attention to the peculiarities found in this specimen. Future collections may reveal intergrading forms between it and the others listed here. *Henry 10290B* (NY), road hill, Mengtsze, Yunnan.

4. Plant only 2.4 dm high, few-headed, with numerous sterile leafy shoots; leaves up to 4.5 cm long, 1.3 cm wide, narrow, and, as in type, slightly rounded at base; leaves, stems, and branches densely setose; heads rather small; involucre about 8 mm high; mature florets and achenes lacking. The pollen grains are irregular, ranging from 22 to 32μ in diameter, averaging 27.5 , which may indicate that this form is a hybrid between two diploid forms, such as the type and m.v. 3 or m.v. 5. *Henry 10290C* (NY), solitary pine mt., Mengtsze, Yunnan.

5. Cauline leaves up to 7.5 cm long, 1.4 cm wide, rather narrow at base, but also somewhat rounded, very finely and shortly pubescent on upper face, sparsely setulose or glabrous beneath; involucre 8–9.5 mm high, the inner bracts sometimes prominently crested; mature florets lacking; achenes 4.5 mm long; pappus 6.5 mm long. The pollen grains are 3-pored and regular in size,

averaging 29μ in diameter, which seems to indicate another diploid form. *Henry 10890D* (US), April 9, Mengtze, Yunnan.

6. Slightly taller and more robust than the type; largest cauline leaves 3 cm long, 7 mm wide, densely setose on both sides; peduncles setulose; involucre 9 mm high, densely setose, the inner bracts sometimes setose-crested; corolla 9–10 mm long; anther tube 3.5 mm long; style branches 1.25 mm long; achenes pale brown, 4–4.5 mm long; pappus white, 6 mm long. Although similar to the type of the species, this plant has very irregular 3-pored pollen grains ranging from 26 to 37μ in diameter (average 32μ). It may therefore be a triploid form, but many fruits appear to have contained developing embryos, which indicates apomictic reproduction. *Maire 1570* (UC), vicinity of Yunnansen, Yunnan.

Relationship

Crepis Phoenix is closest to *C. Bodinieri*, from which it is easily distinguished by its setose stem, branches and involucre, and its shorter and broader, denticulate leaves, as well as in various characters of the flowers and fruits. It is less close to *C. rigescens*, *C. lignea*, and *C. chloroclada*, and it may be considered the most primitive species in this section.

132. *Crepis Bodinieri* Lev.

Bull. Geogr. Bot. 25: 15. 1915. (Fig. 193.)

Perennial, 1.2–7 dm high; caudex woody, rather stout (up to 7 mm wide), vertical or curved, much more than 4 cm long, simple or 2–3-branched; stem or stems erect, terete, dark green, smooth or obscurely pale-striate, branched above or from near base, lower branches when present usually consisting of sterile leafy shoots, the others elongated, somewhat divaricate, \pm leafy, canescent-tomentulose at bifurcations, cymose at summit, few-headed; leaves at base of stem small, scalelike, in mid-region linear, acute or acuminate, sessile, 2.5–8 cm long, 1.5–8 mm wide, dark green, flaccid, margins narrowly retrorsely revolute, canescent-tomentulose on upper surface, lower ones \pm denticulate, the others entire, uppermost bractlike; peduncles 0.3–3 cm long, rather stout, divaricate, bracteate, canescent-tomentulose near head; heads erect, medium, 18–27-flowered; involucre campanulate, 8–9.5 mm high, 3–4 mm wide at receptacle, \pm canescent-tomentulose; outer bracts 8–10, linear, very unequal, the longest $\frac{1}{3}$ – $\frac{2}{3}$ as long as inner ones; inner bracts 12–16, lanceolate, obtuse, ciliate at tip, with white or mottled hairs, glabrous on inner face, becoming carinate dorsally and spongy-thickened at base in fruit; receptacle areolate, glabrous; corolla 11–13 mm long; ligule 1.75 mm wide; teeth 0.3–0.5 mm long; corolla tube 3.5 mm long, glabrous; anther tube 4×0.9 mm dis.; appendages 0.75 mm long, oblong, acute or obtuse; filaments 0.5 mm longer; style branches 1–1.25 mm long, 0.1 mm wide, attenuate at tip; achenes dark brown, 3.75–4.5 mm long, 0.6–1 mm wide, fusiform, subcompressed, shortly attenuate upward, with expanded pappus disk, constricted at the narrow calloused base, about 14-ribbed, ribs nearly equal or 3–4 stronger in marginal achenes, rounded, smooth or very finely spiculate toward summit; pappus white, 5–6 mm long, 1-seriate, nearly equal, rather stiff and brittle, united at base, persistent. Flowering Apr.–May; flowers yellow, ligules reddish on outer face, anthers yellow, style branches yellow or brown in sic.

S.W. China, in N. Yunnan and S. Szechuan, on dry hills and plains, from 1500 to 2550 m altitude.

Although variable in size of plant and in the cauline leaves, the nine specimens seen are fairly uniform in the characteristics peculiar to this species. The more extreme variations, noted below as numbered variants, may all be due to chromosomal differences, except the first (cf. m.v. 1). But until further collections and field observations show that these are representatives of well-established geographic races, it seems sufficient to recognize them merely as minor variants.

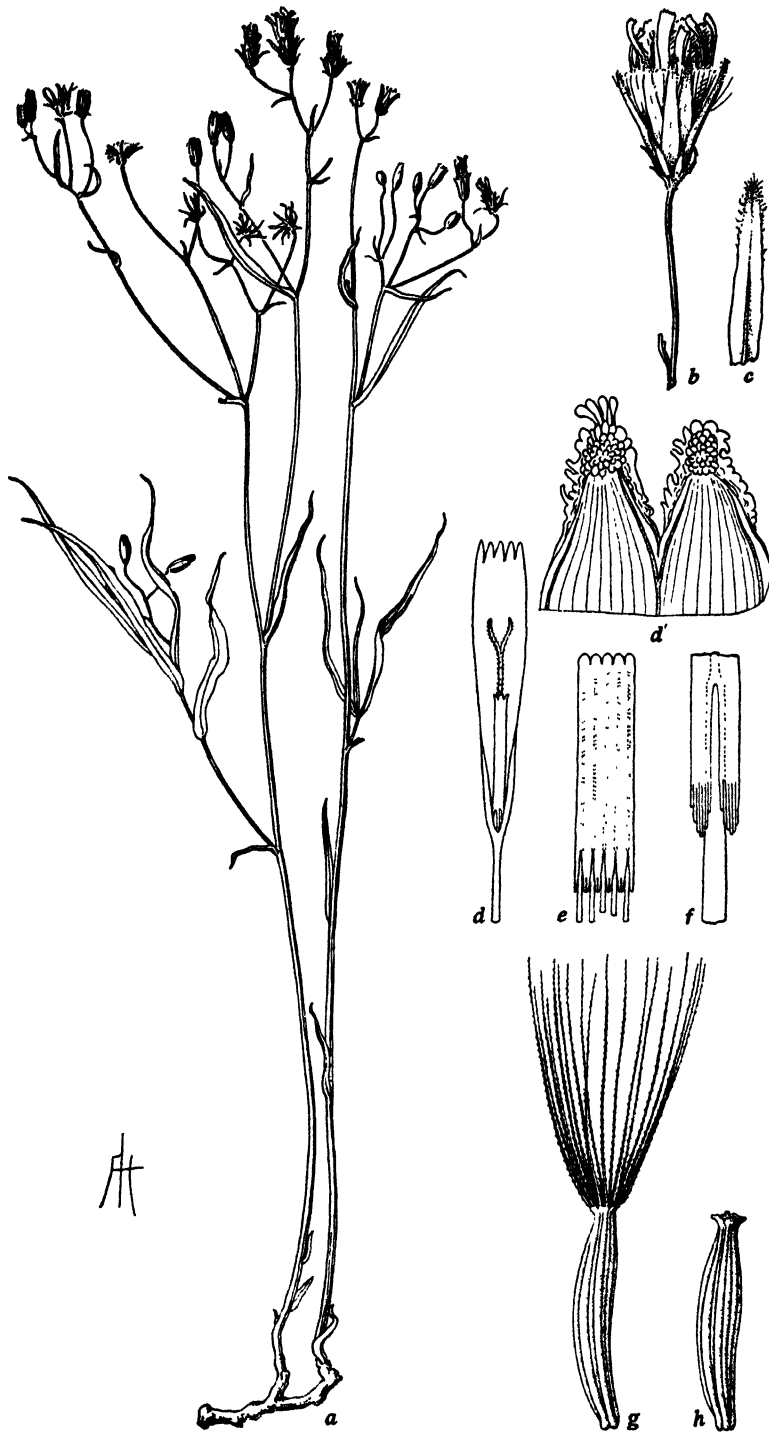


Fig. 193. *Crepis Bodinieri*, a, from type (E); b–f, from *Handel-Massetti 1900* (UC 259889); g, h, from *Handel-Massetti 1879* (UC 259888): a, plant, $\times \frac{1}{2}$; b, flowering head, $\times 2$; c, inner involucre bract, outer face, $\times 4$; d, floret lacking ovary, $\times 4$; d', detail of ligule teeth, $\times 50$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, h, achenes, $\times 8$.

China: Yunnan, Pi-ka-tong, *Maire* in 1912 (E, UCf) type; Yunnan, *Maire* 215 (UC); Yunnan, vicinity of Yunnansen, *Maire* 1569 (UC); N. Yunnan, near Yunnanfu, *Smith* in 1922 (Upsala); *ibid.*, *Schoch* in 1915–1916 (UC) m.v. 3; Yunnan, Kun Ming, 2300 m, *Wang* 62670, 62961 (G); S. Szechuan, Ning-yüan-fu, *Schneider* 1089 (B, UCf); Szechuan, between Ning-yüen and Dötschang, *Handel-Mazzetti* 1900 (US, UC) m.v. 1; Szechuan, near Ning-yüen, *Handel-Mazzetti* 1279 (UC) m.v. 2; Szechuan, Te-chang, *Schneider* 818 (B) m.v. 4.

Minor Variants of *C. Bodinieri*

1. Cauline leaves greatly reduced, those of the mid-region largest, about 3 cm long, 1.5 mm wide, obscurely denticulate, canescent-tomentulose on upper face. The cauline leaves are atypical because of their small size, which gives the plant a very different appearance. But otherwise it is typical, and the nearly regular pollen, averaging 28μ in diameter, indicates that it is a diploid. *Handel-Mazzetti* 1900 (US, UC), Djientschang ("Kientschang") Valley, subtropical reg. between Ningyüen (Lingyüen) and Dötschang on a steppe at Hwang-lienpo, 1570–1650 m, S.W. Szechuan.

2. Plant only 1.2 dm high; otherwise typical. But the pollen grains are irregular ($28\text{--}37\mu$) and large (average 32μ) and there are some 4-pored grains, which indicates that it is a polyploid, possibly a tetraploid form. *Handel-Mazzetti* 1279 (UC), open slope, subtropical reg. near Ningyüen, 1600 m, S.W. Szechuan.

3. Plant 7 dm high; upper cauline leaves up to 15 cm long, 8 mm wide; peduncles 2–13 cm long; heads longer and narrower; involucre 10 mm long, 2.5 mm wide at receptacle; inner bracts 10–12; florets 12–14 mm long; corolla tube glabrous; style branches brown in sic.; achenes 5 mm long, strongly attenuate or coarsely beaked, 12-ribbed; pappus white, 5–6 mm long, unequal. This gigantic form is evidently an unbalanced high polyploid, since the pollen is extremely irregular, ranging from 24μ or smaller to 34μ or possibly larger. From the presence of partly mature achenes it may be inferred that it is an apomict. *Schoch* in 1915–1916 (UC), Yunnan.

4. All cauline leaves reduced to scalelike bracts; peduncles 0.6–3 cm long; heads broader, with more florets; involucre 10 mm long, 4.5 mm wide at receptacle; outer bracts 10–12; inner bracts 12–18; florets 12 mm long; corolla tube glabrous; style branches yellow; achenes 4.5 mm long, strongly attenuate, scarcely beaked, 14-ribbed; pappus white, 5.5 mm long. The very irregular pollen is mostly 3-pored and $22\text{--}29\mu$ in diameter (average $26\text{--}27\mu$), which indicates that this is also an unbalanced polyploid, possibly a triploid apomict. *Schneider* 818 (B), Te-chang, S. Szechuan.

Relationship

Crepis Bodinieri shows most resemblance to *C. rigescens* in the tendency to have the upper cauline leaves long and conspicuous (although in m.v. 1 and 4 the leaves are reduced), but in *C. Bodinieri* the leaves are dark green, flaccid, and tomentulose on the upper face. It is also distinguished from *C. rigescens* by the nearly smooth, dark green stems, the larger heads with more involucre bracts and more numerous florets, the longer florets and anther tubes, and the broader, more attenuate achenes. It is less close to *C. lignea* and *C. chloroclada*; but the dark green herbage and the flaccid, sometimes denticulate leaves and larger heads show some resemblance to *C. Phoenix*.

133. *Crepis rigescens* Diels

Notes Roy. Bot. Gard. Edinb. 25: 202. 1912. (Figs. 194, 195.)

Perennial, 2–4 dm high; caudex woody, slender (up to 4 mm wide), vertical or curved, more than 5 cm long, simple or 2–3-branched; stem or stems erect, glabrous, terete near base, becoming \pm sulcate or angled with prominent yellowish striae, ligneous, branched above or from near base, lower branches often sterile leafy shoots, upper branches cymose, few headed; leaves at base of stem small, scalelike, in mid-region linear, acuminate, sessile, entire (earlier mid-region leaves of young seedlings sometimes denticulate), pale green, coriaceous, 1.5–4 mm wide, margins broadly retrorsely revolute, glabrous, glaucescent; peduncles 0.5–3.5 mm long; heads erect, small, about 12-flowered (18–23-flowered in polyploid forms); involucre cylindric-campanulate, 8–9 mm long, 2–2.5 mm wide at receptacle (2–4 mm wide in polyploids); outer bracts 6, linear or lanceolate, unequal, longest about $\frac{1}{2}$ as long as inner bracts; inner bracts 8–12, lanceolate, usually densely ciliate near

tip, scarious-margined, ventrally glabrous, with median dorsal nerve, becoming carinate, pale spongy-thickened confluent at base in fruit; receptacle areolate, naked; corolla 12 mm long; ligule 2 mm wide; corolla tube 2–3 mm long, glabrous, strongly

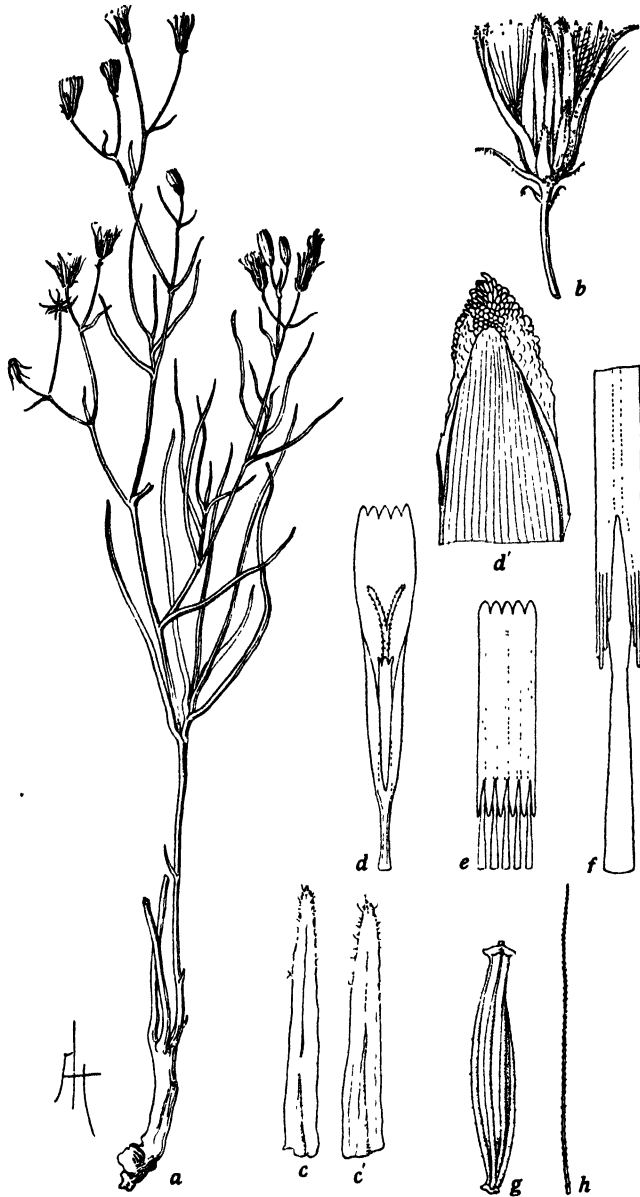


Fig. 194. *Crepis rigescens typica*, a–c', from isotype (P); d–f, from Forrest 14146 (K); g, h, from Rock 4364b (US): a, plant, $\times \frac{1}{2}$; b, immature head, $\times 2$; c, c', inner involucral bract, $\times 4$; d, floret lacking ovary, $\times 4$; d', detail of ligule teeth, $\times 50$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, h, achene and pappus seta, $\times 8$.

nerved; anther tube 3.5–4.5 mm long; style branches 1.75 mm long, 0.1 mm wide; achenes brown, 3.5–4 mm long, subcompressed, fusiform, \pm attenuate upward, with expanded pappus disk and narrow basal callosity, 10–16-ribbed, ribs somewhat unequal, finely spiculate; pappus cream-white, about 5 mm long, 1-seriate, unequal,

some bristles shorter and finer, persistent. Corolla orange yellow; anthers yellow; style branches yellow or green.

S.W. China, in W. Yunnan; and in W. Burma, mountains from 2000 to 3900 m altitude; dry, open, often stony plains and slopes.

That this species is polymorphic is evident even from the scanty collections at present available. The comparison of gross morphology and of the pollen grains reveals the existence of two subspecies, each represented by several specimens, and five other, presumably polyploid, variants each represented by a single specimen (cf. m.v. 1-5).

Key to the Subspecies of Crepis rigescens

Stem branched above the middle or, if branched lower down, the lower branches consisting mostly of short sterile leafy shoots; middle cauline leaves conspicuous, the longest 6-10 cm long, 3-4 mm wide; involucre tomentulose, not gland-pubescent; outer bracts lance-linear, acuminate; inner bracts acuminate.....133, *a. typica*

Stem branched from near the base, the lower branches elongated, floriferous; middle cauline leaves inconspicuous, the longest 3.5-4 or sometimes up to 7 cm long but only 1-2 mm wide; involucre tomentose and usually shortly gland-pubescent; outer bracts lanceolate, acute; inner bracts acute or obtuse.....133, *b. lignescens*

133, *a. Crepis rigescens typica* subsp. nov. Planta 2-4 dm alta; rami inferi brevi foliati steriles; folia caulina conspicua; involucrem tomentulosum, squamis acuminatis; corolla antherae et rami styli flavi; achaenia fusca circa 4 mm longa ad apicem attenuata; pappus albus 5 mm longus.

Plant 2-4 dm high; stem branched above middle or, if branched below, lower branches short, sterile, leafy; flowering branches short, cymose-corymbiform, few-headed; middle cauline leaves conspicuous, up to 6-10 cm long, 3-4 mm wide; involucre canescent-tomentulose; outer bracts lance-linear, acuminate; inner bracts 8-12, acuminate, white-ciliate near apex; corolla 11-12 mm long; ligule teeth 0.3-0.5 mm long; corolla tube 2-2.5 mm long; anther tube 3.6×1 mm dis.; appendages about 0.6 mm long, lanceolate, acute or acuminate; filaments 0.6-1 mm longer in different florets, strongly attenuate from base of filament to appendages; style branches yellow. See fig. 194.

Yunnan: Lichiang Valley, N. end, 27° 10' N., 2700 m, *Forrest 2192* (P, UCf) isotype; Salween divide, Mekong R., 28° 12' N., 3900 m, *Forrest 14146* (K); E. slopes of Likiang Snow Range, *Rock 4364b* (US, UCf); Yungpeh, *Forrest 20677* (B, US, UC), young plants, no flowers or fruits; locality?, *Forrest 10588* (K); Pe-yen-tsin, *Chan Cheng 71* (B) m.v. 1; Yunnansen, *Maire 1571* (K) m.v. 3; without definite locality, *Maire 215* (NY) m.v. 4; Yunnansen, *Cavalerie 7924* (K) m.v. 5; Kang pu, Wei-si Hsien, *Wang 64413* (G); Yunnan, *Yü 5288, 6040* (G) near m.v. 3; N.W. Yunnan, Likiang Snow Range, Ahsi, open ledges along the Yangtze R., *Ching 20744* (G).

Minor Variants of C. rigescens typica

1. Plant more than 4 dm high; heads 15-flowered; involucre 10 mm long, 3 mm wide at receptacle; nearly mature achenes 5 mm long, very gradually attenuate to summit, with expanded pappus disk; pappus 5-6 mm long. The pollen grains range from 29 to 31μ , averaging 30μ in diameter, which indicates that this may be a triploid form of *C. rigescens typica*. *Chan Cheng 71* (B) Pe-yen-tsin, N.W. Yunnan.

3. Heads broader than usual in subsp. *typica*, containing up to 23 achenes; involucre 3-4 mm wide at base; achenes 3.5-4 mm long, 0.5-0.6 mm wide, slightly attenuate, constricted below the expanded pappus disk, 16-18-ribbed. There are no flowers on this specimen, but the broader heads, with more numerous fruits than usual, indicate that it may be a polyploid of some sort, since most of the other forms suspected, from pollen characters, of being polyploids have larger heads. *Maire 1571* (K), vicinity of Yunnansen, Yunnan.

4. Stem branched from near base; cauline leaves narrower, 0.75-1.5 mm wide; heads about 18-flowered. The rather scanty pollen is 3-pored but very irregular, ranging from 25 to 35μ in diameter. This may indicate that the plant is an unbalanced polyploid. *Maire 215* (NY), Yunnan.

5. Plant robust, 4.5 dm high and branched from near base; the stems and extremely narrow leaves dark green; leaves about 0.5 mm wide; heads narrow but 20-23-flowered; peduncles and

involucres sparsely canescent-tomentulose; corolla 10 mm long; anther tube 3.5 mm long; achenes lacking. The pollen is abundant and 3-pored but very irregular with many large grains (range $26\text{--}37\mu$). In the narrow involucres and very narrow, coriaceous leaves this plant simulates *C. rigescens typica*; but the dark green herbage and sparsely tomentulose involucres suggest *C. Bodinieri*. Possibly it is an amphidiploid hybrid between the two species. *Cavalerie 7924* (K), Yunnansen dist., Yunnan.

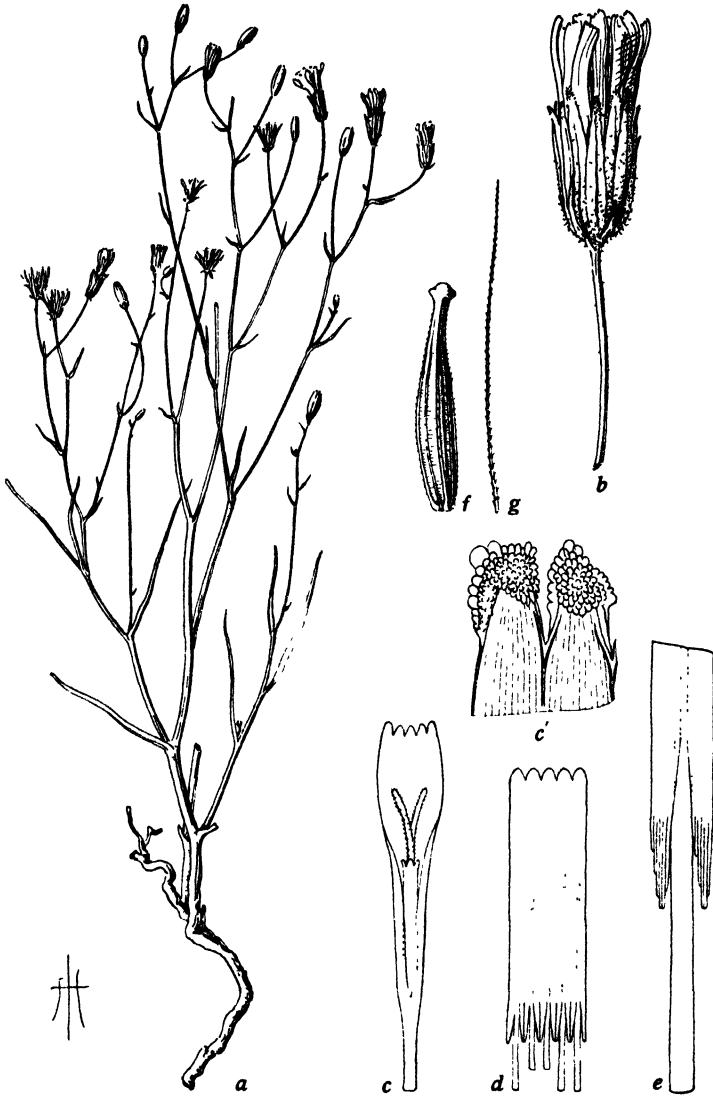


Fig. 195. *Crepis rigescens lignescens*, from type (B): a, plant, $\times \frac{1}{2}$; b, flowering head, $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule teeth, $\times 50$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, g, achene and pappus seta, $\times 8$.

133. *b. Crepis rigescens lignescens* subsp. nov. Planta circa 2 dm alta; rami inferi elongati floriferi; folia caulina parva; involucrium tomentosum glandulosum, squamis exterioribus lanceolatis acutis, interioribus obtusis; corolla et antherae flavae; rami styli virides; achaenia fusca circa 4 mm longa ad apicem attenuata; pappus albus 5 mm longus.

Plant about 2 dm high; stem branched from near base, lower branches elongated,

strict, floriferous and with occasional sterile leafy branchlets, aggregate inflorescence cymose-corymbiform; cauline leaves inconspicuous, up to 4 or 5 or sometimes 7 cm long, about 2 mm wide; involucre canescent- or fuscous-tomentulose and usually shortly gland-pubescent, especially at base; outer bracts lanceolate, acute; inner bracts 10–12, obtuse or sometimes acute, densely ciliate near apex with finely mottled hairs; corolla 12 mm long; ligule teeth 0.25–0.35 mm long; corolla tube 3 mm long; anther tube 4.5×1.25 mm dis.; appendages 0.7 mm long, narrow, acuminate; filaments unequal, 0.4–0.75 mm longer; style branches green. Flowering Apr. See fig. 195.

This subspecies is reminiscent of *Crepis lignea* in size and habit of the plant and its somewhat stouter, much branched stem, with the lower branches elongated, strict and floriferous. The occasional leafy, sterile shoots are not found in *C. lignea*, and the cauline leaves are intermediate between *C. lignea* and *C. rigescens typica*; the short gland hairs on the involucre are like those of *C. lignea*; and the involucre bracts resemble those of *C. lignea*, even to the mottled cilia on the inner bracts. But the flowers and fruits are more like those of *C. rigescens*. This suggests that subsp. *lignescens* is a hybrid derivative from *C. lignea* \times *C. rigescens*. In the type of subsp. *lignescens*, cited below, the pollen grains range from 28 to 31μ and average 30μ in diameter, as compared with 24–28 μ , average about 26 μ , in a specimen of subsp. *typica* (Forrest no. 14146). In the latter the stomata average about 31μ in length of the guard cells. These stomatal and pollen measures of subsp. *typica* correspond with those of *Crepis Raulini*, *C. oporinoides*, and *C. nicaeensis*, all of which are known to be diploid species. The equally regular but larger pollen grains of subsp. *lignescens* indicate that it is a tetraploid, and it might well be an amphidiploid produced from the interspecific hybrid above mentioned. This evidence seems sufficient to warrant the recognition of this form as a subspecies.

Yunnan: hills around Tengyueh, open stony clayey pasture, 2100 m, *Forrest 26307* (B, UCf) type; *ibid.*, *Forrest 26307a* isotype, *26307b* m.v. 2 (US); *ibid.*, *Forrest 26307* (UC) isotype; "E. Tibet and S.W. China," *Forrest 26307* (NY, compared with isotype in Herb. UC); Ta-li Hsien, 2540 m, *Wang 63506* (G) near m.v. 2. **Burma:** Haka, dry slopes after fires, 1920 m, *Dickson 7452* (G).

Minor Variant of C. rigescens lignescens

2. Plant about 3 dm high; heads more than 12-flowered; involucre yellowish tomentose at base, not at all glandular; achenes lacking. The larger size of this plant and broader heads with more numerous florets suggest that it is a polyploid form. Its pollen grains are large and very irregular, 28–37 μ , average 34 μ , which indicates that it is a high polyploid and possibly an apomict. *Forrest 26307b* (US), open pasture, 2100 m, hills around Tengyueh, N.W. Yunnan.

Relationship

Crepis rigescens is closest to *C. Bodinieri*, from which it is clearly distinguished by the pale yellowish-green color of the herbage (except in occasional variants), the sulcate or angular stems and branches, the narrower, coriaceous leaves with broadly revolute margins, and the smaller, fewer-flowered heads with fewer involucre bracts. *C. rigescens* is less close to *C. lignea* and still less close to *C. Phoenix*. But it seems probable that *C. rigescens* may have been one of the parents of *C. chlorocladia*; also that *C. rigescens typica* crossed with *C. lignea* to produce *C. rigescens lignescens*. The distributional area of *C. lignea* includes that of *C. rigescens*.

134. *Crepis lignea* (Vaniot) comb. nov.

(Pl. 14. Fig. 196.)

Perennial, 1.5–4 dm high; caudex woody, 0.5–1.5 cm wide at the divided summit, contracted below into a slender elongated vertical or oblique neck which is enlarged and branched below, probably with deeply penetrating roots; stems stiffly erect,

woody, terete, dark or pale green, remotely branched from near base upward, glabrous or (m.v. 2 and 3) hispidulous; branches numerous, fastigate, sulcate and angular, the lower cymosely 2–4-branched, the upper pedunculate, branching angles narrow, aggregate inflorescence congested, cymose-corymbiform; leaves of caudex and lower stem inconspicuous, scalelike, triangular, acute, subamplexicaul, in mid-region up to 3 cm long, filiform, entire, broadened at base, the uppermost linear, bractlike; peduncles 0.5–5 cm long, slender, erect, 1–2-bracteate, glabrous except m.v. 2 and 3 or shortly gland-pubescent near head; heads erect, rather small, 7–12-flowered; involucre cylindric-campanulate, 7–9 mm high, 1.5–2.5 mm wide at re-

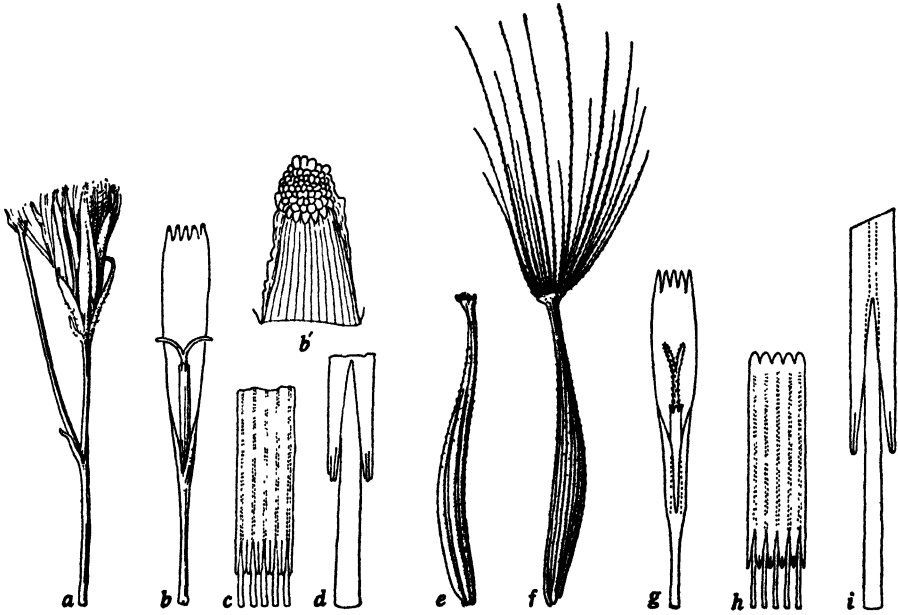


Fig. 196. *Crepis lignea*, a–f, from Henry 10165a (NY); g–i, from type (E): a, head, peduncle, and branchlet, $\times 2$; b, floret lacking ovary, $\times 4$; b', detail of ligule tooth, $\times 50$; c, anther tube, $\times 8$; d, detail of appendages, $\times 32$; e, f, achenes, $\times 8$; g, floret lacking ovary, $\times 4$; h, anther tube, $\times 8$; i, detail of appendages, $\times 32$.

ceptacle in fruit, glabrous, tomentulose or very shortly gland-pubescent, becoming lax in fruit; outer bracts 5 or 6, unequal, longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as inner bracts, lance-linear, acute or acuminate; inner bracts 8–11, lanceolate, obtuse, ciliate at tip, with many fine mottled hairs, scarious-margined, ventrally glabrous and strongly 3–5-nerved, dorsally 1-nerved, becoming carinate and spongy-thickened near base in fruit; receptacle areolate, naked; corolla 10–11 mm long; ligule 1.5 mm wide; teeth 0.4–0.8 mm long; corolla tube 3 mm long, glabrous, strongly veined; anther tube 3.5×0.9 mm dis.; appendages 0.6 mm long, narrow, acuminate; filaments 0.6 mm longer; style branches about 1 mm long, 0.1 mm wide; achenes brown, 4–5 mm long, fusiform, strongly attenuate upward or coarsely beaked, the beak $\frac{1}{5}$ – $\frac{1}{3}$; the length of the whole achene, with expanded pappus disk, constricted at the pale-calloused hollow base, subterete or subcompressed, 10–12-ribbed, ribs rounded, nearly equal or alternate ribs sometimes weaker, finely spiculate; pappus cream-white or white, 4–5 mm long, in 1 series of coarser and finer setae, soft or somewhat brittle, persistent. Flowering Mar.–June; ligules yellow, anthers yellow, style branches probably green, or yellow in some forms (brown, gray, or blackish in sic.).

Lactuca lignea Vaniot, Bull. Acad. Geogr. Bot. 12: 318. 1903.

L. Klossii S. Moore, Jour. Nat. Hist. Soc. Siam, 4: 148. 1921.

S.W. China, in Yunnan, S.W. Kweichow and S.W. Szechuan; N. Siam and S. Annam; dry hillsides and rocky slopes from 1000 m to 3000 m altitude; waysides and cultivated fields. Type locality, Kweichow, between Hin-y-fou and the Hoa-Kiang River.

Typical forms also occur at Mengtsze, in Yunnan, and probably in Szechuan. Like the type, these plants have fairly regular 3-pored pollen grains which average $26\text{--}27\mu$ in diameter. Certain variants, each of which is known from only a single locality (cf. m.v. 1, 2, 3) must be considered. Like the typical form, they appear to be diploids, and they may differ from the type in certain genes. But there is some evidence of genic diversity even among the otherwise typical forms, such as dark green and pale green stems. Therefore, until more is known about the distribution and constancy of these variants, one is hardly warranted in recognizing them as subspecies. Certain other variants, found at Mengtsze, Yunnanfu, and in the Likiang Mts., in W. Yunnan (cf. m.v. 5, 6, 7), appear to be polyploids, and they may represent apomictic races. But, for the same reasons, they are treated here merely as numbered variants.

China: Kweichow, between Hin-y-fou and Hoa-Kiang R., here and there in cultivated fields, *Bodinier 1561* (E, UCf) type; Yunnan, Mengtsze, dry sandy downs bordering the plain and on hill flanks, *Hancock 32* (K); Mengtsze, *Henry 10165* part (K, NY, UCf); Yunnan, *Forrest 7170* (K); Yunnanfu, waysides, *Schoch 110* (US) m.v. 1; Yunnan, Szemao, mountains in grass, 1500 m, *Henry 13798* (K, UCf); Yunnan, Ping-pien-hsien, *Tsai 62038* (G); Yunnan, Hoa-ngi-tehai, 2500 m, dry rocks, *Maire 3618* (UC) m.v. 2, 3; *ibid.*, *Maire 3618* (NY) m.v. 2; Yunnan, Likiang dist., east slopes of Likiang Snow Range, 3000 m, *Rock 4364a* (US) m.v. 4; Yunnansen, *Maire 1568* part (B, UC) m.v. 5; *ibid.*, *Maire 1568* part (UC) m.v. 7; Mengtsze, *Henry 10165* part (NY, US) m.v. 6; Szechuan, Ning yüan fu, Lu shan, *Schneider 867* (G) near m.v. 5. **S. Annam:** Langbian, Dalat, 1515 m, *Kloss* in 1918 (RM, UCf), as *Lactuca Klossii* S. Moore; Langbian Mts., Dran, 1000–1200 m, *Chevalier 40523* (P, UCf). **Siam:** Chungmai (Chiengmai ?), Doi Soetep, 1200–1500 m, open grassy jungle, *Kerr 1108* (K, UCf, P).

Minor Variants of *C. lignea*

1. Plant only 1.5 dm high; stems slender; heads small, 7–8-flowered; achenes 4–4.5 mm long, coarsely beaked, sometimes reddish-brown; pappus 4–5 mm long, white. These plants differ from the type mostly in quantitative characters. The pollen grains are regular, 3-pored, and average $25\text{--}26\mu$ in diameter, which indicates that they are diploids. These plants appear to have been mutilated by grazing, and the note of the collector that they occurred along a road or path may indicate that they grew under conditions unfavorable for even this hardy species. Therefore, until it is known whether seeds from such plants will reproduce the reduced form, they must be suspected of being merely environmental modifications. *Schoch 110* (US), along ways, Yunnanfu, Yunnan.

2. Plant only 1.5–2.3 dm high and glandular-hispidulous throughout; stems and branches somewhat stronger than in m.v. 1 but more slender than in typical forms, dark green; heads also intermediate in size, about 10-flowered; involucre tomentulous, glandular-hispidulous and gland-pubescent at base; achenes 3–4.5 mm long, coarsely beaked; pappus 4–4.5 mm long, white. These plants also have the appearance of having been repressed by conditions of growth, but their strikingly different indumentum indicates that they are genetically diverse from the type of the species. Only controlled garden tests can reveal the amount of such diversity. The pollen grains are regular, 3-pored, and average about 25μ in diameter. (Pl. 14, b.) *Maire 3618 a, b, c* (UC, NY), dry rocks, 2500 m, Hoa-ngi-tehai, Yunnan.

3. Plant 2.3 dm high and glandular-hispidulous throughout; branching angles of upper branchlets narrow, as in type, but lower branches more divaricate, thus giving a broader spread to the plant; stem and branches nearly as robust as in typical forms, strongly sulcate and pale yellowish-green; heads as in m.v. 2; involucre less hispidulous; outer bracts shorter, the longest less than $\frac{1}{3}$ as long as inner; immature achenes about 4 mm long, coarsely beaked; pappus 5 mm long, cream-white. The one specimen seen differs from the type not only in its smaller size but also in habit, color of stem, and branches, and in indumentum. But these differences may be attributable to relatively few genic differences and the plant seems to have been collected at the same station

as m.v. 2. The pollen is regular, 3-pored, and averages about 28μ in diameter, which indicates that this plant is also a diploid. Thus, it appears that at Hoa-ngi-tehai there exists a genetically diverse population of diploid plants of this species. Field studies on the nature and amount of variation in this population and tests of the constancy of the various forms found there would be necessary before reaching any conclusions about the taxonomic status of these forms. (Pl. 14, c.) *Maire 3618d* (UC), dry rocks, 2500 m, Hoa-ngi-tehai, Yunnan.

4. More slender throughout than the type; heads somewhat smaller, about 9-flowered; florets, achenes and pappus typical. The pollen of this plant is very irregular and both 3-pored and 4-pored grains are present. The grains average $28-29\mu$ in diameter. It is probable that this is a triploid plant and, since it comes from a station far removed from all other known stations, it is possible that it represents an apomictic race. (Pl. 14, d.) *Rock 4364a* (US), Ma Huang paddock, 3000 m, E. slopes of Likiang Snow Range, Yunnan.

5. Plants 1.8–2.8 dm high and somewhat more slender; heads typical, 7–11-flowered; corolla tube 2–2.5 mm long, glabrous (fungus hyphae present); anther tube 3.5 mm long; involucre tomentulose, not gland-pubescent; pappus 5 mm long, white. The pollen is irregular, with 3-pored and 4-pored grains present, and averages 32μ in diameter. This is probably another triploid form, and it may be an apomict. *Maire 1568* part (B, UC), vicinity of Yunnansen, Yunnan.

6. Plant taller, up to 4 dm high, more slender and somewhat more open; stems and branches somewhat flexuous; heads narrower, 7–10-flowered; corolla tube glabrous; involucre \pm hispidulous; achenes 3.5 mm long; pappus 6 mm long, cream-white. The pollen is irregular, mostly 3-pored, and averages 29μ in diameter. This form may be another triploid apomict. (Pl. 14, f.) *Henry 10165* part (US, NY), Mentgsze, Yunnan.

7. Plant 4 dm high and more robust; middle cauline leaves up to 3 cm long; branchlets canescent-tomentose; peduncles gland-pubescent; heads typical or slightly larger, up to 14-flowered; involucre hispidulous; immature achenes 4.5 mm long; pappus 5 mm long, cream colored. The pollen is very irregular, with a few 4-pored grains present, and averages 32μ in diameter. This is probably a tetraploid form. (Pl. 14, g.) *Maire 1568* part (UC), vicinity of Yunnansen, Yunnan.

Relationship

The classification of *Crepis lignea* under *Lactuca* sec. *Ixeris* by Vaniot must have been based on the superficial appearance of the plant, together with the few-flowered heads and somewhat *Ixeris*-like achenes. But no true *Ixeris* species are known to have the strong woody base and ligneous stems of this species, and the involucre is not right for *Ixeris*, since the outer bracts are narrow and remote, not ovate and imbricate, and they are very unequal. Furthermore, the unequally ribbed achenes resemble those of other species of this section more closely than those of any species of *Ixeris*. In many herbarium specimens of this species the florets are not well preserved, having become infested with a fungus. The minute fruiting bodies are conspicuous under a compound microscope. The hyphae are especially apt to be developed in a mass near the summit of the corolla tube, thus giving the appearance of the localized pubescence so characteristic of many species of *Lactuca*. But in 12 specimens of *C. lignea*, in which the florets were carefully examined, the corolla tube was always glabrous.

Crepis lignea resembles *C. chloroclada* in its habit and in the rather small heads, and it is possible that *C. lignea* is one of the parents of that little-known species. Next stands *C. rigescens*, from which *C. lignea* is very distinct in its fastigiate habit, very small leaves, smaller heads, and beaked achenes. It is less close to *C. Bodinieri* and to *C. Phoenix*.

135. *Crepis chloroclada* Collett et Hemsl.

Jour. Linn. Soc. 28: 78. 1890. (Pl. 15. Fig. 197.)

Perennial, about 3.5 dm high; caudex woody, 1.5 cm wide, attenuate into a woody taproot, 6–8-divided at summit, each division bearing 2–4 stems; stems many, erect, stiff, woody, terete, remotely paniculately branched from near base; branches numerous, fastigiate, strongly sulcate or angular, green, cymosely branched below, dichotomous above, with wide branching angles, aggregate inflorescence corymbiform, but

many of the ultimate branchlets leafy and sterile; caudical and lower cauline leaves scalelike; middle cauline leaves about 1 cm long, subulate or bractlike; upper cauline leaves 2.5–4 cm long, 1–3 mm wide, linear, acuminate, glabrous, coriaceous, margins strongly retrorsely revolute; peduncles 0.5–2.5 cm long, slender, somewhat

thickened, sulcate and gland-pubescent near head; heads rather few, erect, small, 7–10-flowered; involucre 6–7 mm long, 1–2 mm wide; outer bracts 5, nearly equal, about 2 mm long, 0.5 mm wide, lanceolate, acute, \pm gland-pubescent; inner bracts 8, lanceolate, obtuse, ventrally glabrous, dorsally gland-pubescent, becoming strongly carinate and coriaceous, the gland hairs becoming thickened and setiform; receptacle glabrous; unopened florets 5.5 mm long; corolla tube about 1 mm long, glabrous; anther tube 2.5 mm long, the appendages short, acute; style branches about 0.6 mm long; immature achenes about 2.5 mm long, strongly attenuate at summit, with expanded pappus disk, subcompressed, about 10-ribbed, ribs somewhat unequal; pappus white, 3–4 mm long, 1–2-seriate, of alternate coarser and finer setae. Flowering May.

Known only from the type locality.

Monomorphic.

E. Burma: Shan Hills, 1200 m, Collett 659 (K, UCf) type.

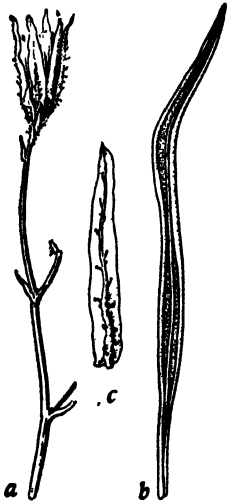


Fig. 197. *Crepis chloroclada*, from type (K): a, branchlet and head, $\times 2$; b, cauline leaf, $\times 2$; c, inner involucre bract, outer face, $\times 4$.

Relationship

Since the type specimen lacks mature florets and achenes, the relationship of *Crepis chloroclada* cannot be definitely determined. The type is apparently a triploid, since the pollen grains are both 3-pored and 4-pored and are 25–26 μ in diameter. Its many woody, fastigiate stems and branches and small heads suggest affinity with *Crepis lignea*. But it is very distinct from that species in the wide branching angles of the upper branchlets, in the presence of many leafy, sterile branches among the inflorescence, in the larger size of the uppermost leaves, in the setulose involucre bracts in older heads, and in the presumably smaller achenes and shorter pappus. In fact, the subcompressed and somewhat unequally ribbed immature achenes are reminiscent of *Crepis rigescens*, and the habit and leaves are rather similar, although the heads in *C. rigescens* are much larger. These observations suggest that *C. chloroclada* might be a hybrid form of some sort derived from the natural crossing of *C. rigescens* and *C. lignea*.

SECTION 19. PHAECASIUM

The 6 species of this section exhibit a remarkable range of variation in type of root and length of the life cycle. Yet they are more closely related to one another than to any other section, and their distribution (fig. 198) is consistent with the morphological and cytological evidence. Four of the species are restricted to the Syria-Palestine-Cyprus region, and the one widely distributed species, *C. pulchra*, also occurs in that region. The sixth species, *C. Stojanovi*, is a local endemic of S.E. Bulgaria. Five of the 6 species have almost identical karyotypes; the sixth has not

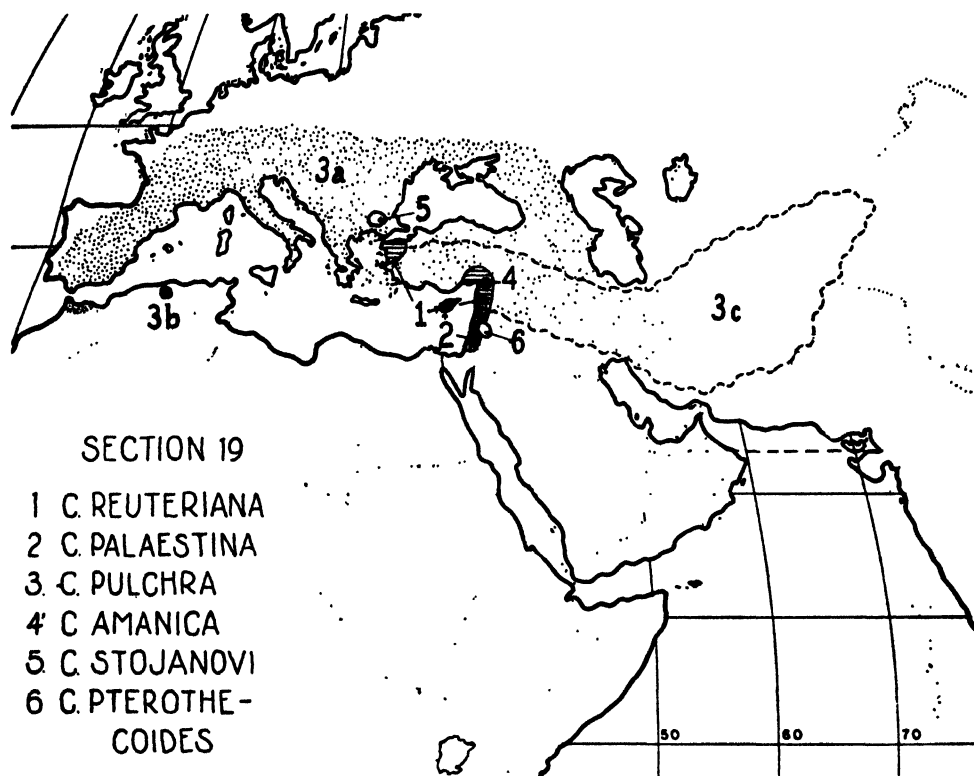


Fig. 198. Geographic distribution of the 6 species in sec. 19. Single known stations are shown by solid circles. Based on Goode Base Map No. 201 HC. By permission of the University of Chicago Press.

been examined cytologically. The 6 species fall into 2 subgroups: (1) *C. Reuteriana*, *C. palaestina*, *C. pulchra*, and *C. pterothecoides*; (2) *C. amanica* and *S. Stojanovi*. Furthermore, in spite of their diversity in respect to the features mentioned above, these species actually exhibit strong resemblances in habit, leaf shape, and the specialized involucre, as well as the peculiar fine dense pubescence of the corolla tube and the extremely fine soft pappus setae.

(1) *C. Reuteriana* is the only perennial species in the section, and it has a strong woody subterranean stem which usually bears strong lateral roots near the caudex. This peculiar type is intermediate between the typical rhizome of the most primitive species in the genus and the deeply penetrating taproot of the other 5 species. These features and the uniform, broadly ribbed achenes, which are larger and more broadly ribbed in subsp. *Egiana*, make this the most primitive species in the section. *C. Reuteriana* also exhibits some resemblance to *C. bupleurifolia* of sec. 10. *C.*

palaestina stands next, and on the basis of size alone it might appear to be more primitive. But the annual habit and the triform, specialized achenes definitely mark it as more advanced. Like *C. Reuteriana*, *C. palaestina* is restricted to the center of distribution for this section. *C. pulchra*, although often producing a large-sized plant under favorable conditions, is actually much more reduced than *C. palaestina*, especially in its florets and achenes, which are also triform or sometimes biform. *C. pulchra* is polymorphic, comprising 3 subspecies and many variants; and it is the only widespread species in the section. *C. pterothecoides* is a very precocious desert annual. The plant is small, and the achenes, although uniform, are usually more or less definitely beaked. So far as known, it has a restricted distribution in the Anti-Liban-Jebel Druz region bordering the Syrian desert on the west. Thus, in these 4 species we find an excellent illustration of several of the evolutionary trends which are characteristic of *Crepis*: (a) in duration of life cycle—perennial, slowly developing annual, and precocious annual; (b) in size of plant—large, medium, small; (c) in specialization of achenes—uniform and unbeaked or bi- or triform and unbeaked or uniform and beaked; (d) in distribution—restricted endemics occurring under conditions of summer moisture (*C. Reuteriana* is montane, and *C. palaestina* grows in shady places at low elevations); widely distributed and ruderal (*C. pulchra*); and a restricted xerophytic endemic (*C. pterothecoides*).

(2) *C. amanica* is known only from the type specimen, although it grew in the Amanus Mts., a region which has been visited by a good many botanists, including Dr. A. Eig and M. Zohary, who made an expedition for the present author in 1931. They reached the Amanus Mts. in May, and went on to the Cilician Taurus. Hence, it would not seem that *C. amanica* is at all common in that region. Perhaps it is a very local endemic, like *C. Stojanovi* of Bulgaria. The latter species has been cultivated at Berkeley, and it unquestionably belongs in this section, although the uniform beakless achenes differ strikingly in shape from those of the first four species. *C. amanica* appears to be intermediate between *C. Stojanovi* and *C. pterothecoides* in a number of characters, but the achenes are more like those of *C. Stojanovi* and the broadly rounded ribs resemble those of *C. bupleurifolia* of sec. 10. *C. Stojanovi* and *C. pulchra* have been crossed artificially, but the hybrids were completely sterile. Hybrids between *C. pulchra* and *C. Reuteriana* had very low fertility; but those between *C. pulchra* and *C. palaestina* were moderately fertile. This agrees with the morphological evidence which indicates that these two species are closer genetically than any other two in the section. This fact emphasizes the purely artificial nature of the distinctions on which the two genera, *Phaeacasium* Cass. and *Cymboseris* Boiss., were based.

Key to the Species of Section 19

- Plant perennial; achenes 15–20-ribbed. 136. *C. Reuteriana*, p. 651
- Plant annual; achenes striate or 10-ribbed.
- Achenes biform, or if diverse marginal achenes absent, then those present of two colors or some spiculate and the others smooth.
- Involucres 12–16 mm long, 5–8 mm wide; corolla 15–19 mm long; marginal achenes broad at base, gradually attenuate to apex; inner achenes with a swollen hollow base. 137. *C. palaestina*, p. 656
- Involucres 8–11 (12) mm long, 3–5 mm wide; corolla 5–12 mm long; marginal achenes narrow at base, wider at middle, attenuate at apex; inner achenes narrow at base 138. *C. pulchra*, p. 661
- Achenes uniform.

Involucres 7–8 mm long; outer bracts 6–10, very short; achenes 3–4 mm long, 0.7–1 mm wide, beakless.

Involucres and peduncles glabrous or peduncles sparsely tomentulose; inner bracts glabrous on inner face; achenes fusiform, nearly equally constricted at the narrow apex and base, the ribs narrower.....140. *C. Stojanovi*, p. 669

Involucres and peduncles densely gland-pubescent; inner bracts pubescent on inner face; achenes more strongly attenuate toward the base than the apex, apex and base wider, the ribs broader.....139. *C. amanica*, p. 668

Involucres 10–14 mm long; outer bracts 10–14, the longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner; achenes 6–9 mm long, 0.3–0.5 mm wide, mostly beaked. 141. *C. pterothecoides*, p. 671

136. *Crepis Reuteriana* Boiss.

Diagn. Pl. Orient. Nov. ser. 1, 11: 55. 1849. (Figs. 199–201.)

Perennial, 0.8–7.5 dm high; rootstock or subterranean stem strongly woody, vertical, oblique, or horizontal, bearing strong lateral roots near the caudex; caudex narrow and 1-stemmed in young plants, up to 3 cm wide, \pm divided, and many-stemmed in old plants; caudical leaves 4–18 cm long, 1–3 cm wide or wider, oblanceolate, lyrate-runcinate-pinnatifid or coarsely dentate, acute or obtuse, petiolate, pubescent or hispidulous; lower 1 or 2 cauline leaves similar or entire, or all reduced and bractlike; stem or stems erect, terete, striate, \pm pubescent, strictly or divaricately branched from near base or above, lower branches elongated, 1–4-headed, aggregate inflorescence corymbiform; peduncles 1–15 cm long, slender; heads erect, medium, 20–40-flowered; involucre cylindric, the outer bracts short, lanceolate, acuminate, narrowly white-margined, the inner bracts lanceolate, acute, at least the innermost membranous-margined; ventrally pubescent on upper half with very fine white hairs, these sometimes obscure or absent, strongly carinate and spongy-thickened dorsally in fruit, ultimately reflexed; receptacle areolate, shortly and sparsely white-ciliate; ligules yellow; corolla tube densely pubescent with several-celled acicular or crinkled hairs 0.1–1 mm long; achenes tawny or greenish-yellow, fusiform, with scarcely expanded pappus disk and narrowly calloused hollow base, 15–20-ribbed, ribs weak, rounded, smooth or very finely spiculate under lens; pappus white, 5–6 mm long, 2–3-seriate, very fine, soft, deciduous. Chromosomes, $2n = 8$.

W. and S. Asia Minor, Syria, N. Palestine, and Cyprus (cf. subspp. *typica*).

This species comprises two well-marked subspecies, with identical karyotypes, which occur largely at different altitudes in the mountains of Liban, S.W. Syria, but which overlap and apparently hybridize naturally, since cultures grown at Berkeley from seeds collected in the wild contained intergrading forms. In N.W. Syria and Cilicia both subspecies also occur together with intergrading forms, but little is known about their altitudinal distribution.

Key to the Subspecies of Crepis Reuteriana

Involucres glabrous, or sparsely pubescent with glandless setiform hairs up to 1 mm long; pubescence of leaves and stems glandless, or \pm glandular; style branches green; achenes tawny, 4–5 mm long, 0.5 mm wide.....136, *a. typica*

Involucres densely gland-pubescent with very short fine hairs, or glabrous; pubescence of leaves and stems \pm glandular; style branches yellow; achenes greenish-yellow, 5–7 mm long, 1–1.25 mm wide.....136, *b. Eigia*

136, *a. Crepis Reuteriana typica* Babc., Univ. Calif. Publ. Bot. 19: 402. 1941. Stems 3–7.5 dm high; rootstock in young plants elongated, slender, often disappearing in older plants, being replaced by numerous strong lateral roots at the crown; caudical leaves pubescent with pale glandless hairs often denser and longer on

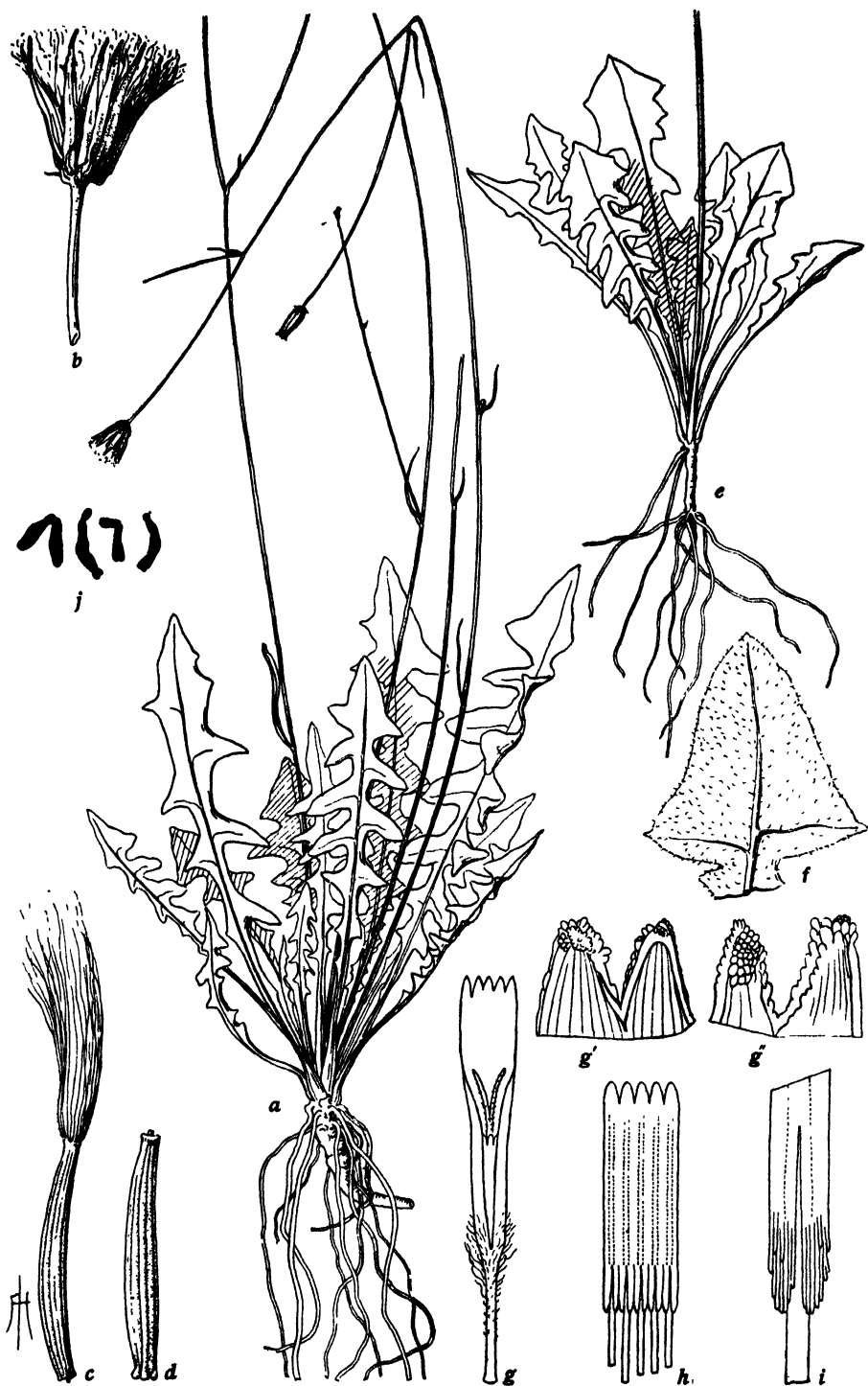


Fig. 199. *Crepis Beuteriana typica*, a, from type (Bo); b-d, from Balansa 255 (Bo); e-i, from Gaillardet in 1858 (US 132823); j, from hort. genet. Calif. 2218 (grown from seeds received from Palestine through Dr. M. Navashin): a, plant, $\times \frac{1}{2}$; b, head, $\times 2$; c, d, 2 achenes, 1 with pappus, $\times 8$; e, lower part of a young plant showing lower root system and 2 fibers developed at crown of caudex, $\times \frac{1}{2}$; f, terminal lobe of caudical leaf, $\times 1$; g, floret lacking ovary, $\times 4$; g', inner face, and g'', outer face of 2 ligule teeth, $\times 25$; h, anther tube, $\times 8$; i, detail of appendages, $\times 32$; j, somatic chromosomes, $n = 4$, $\times 1250$.

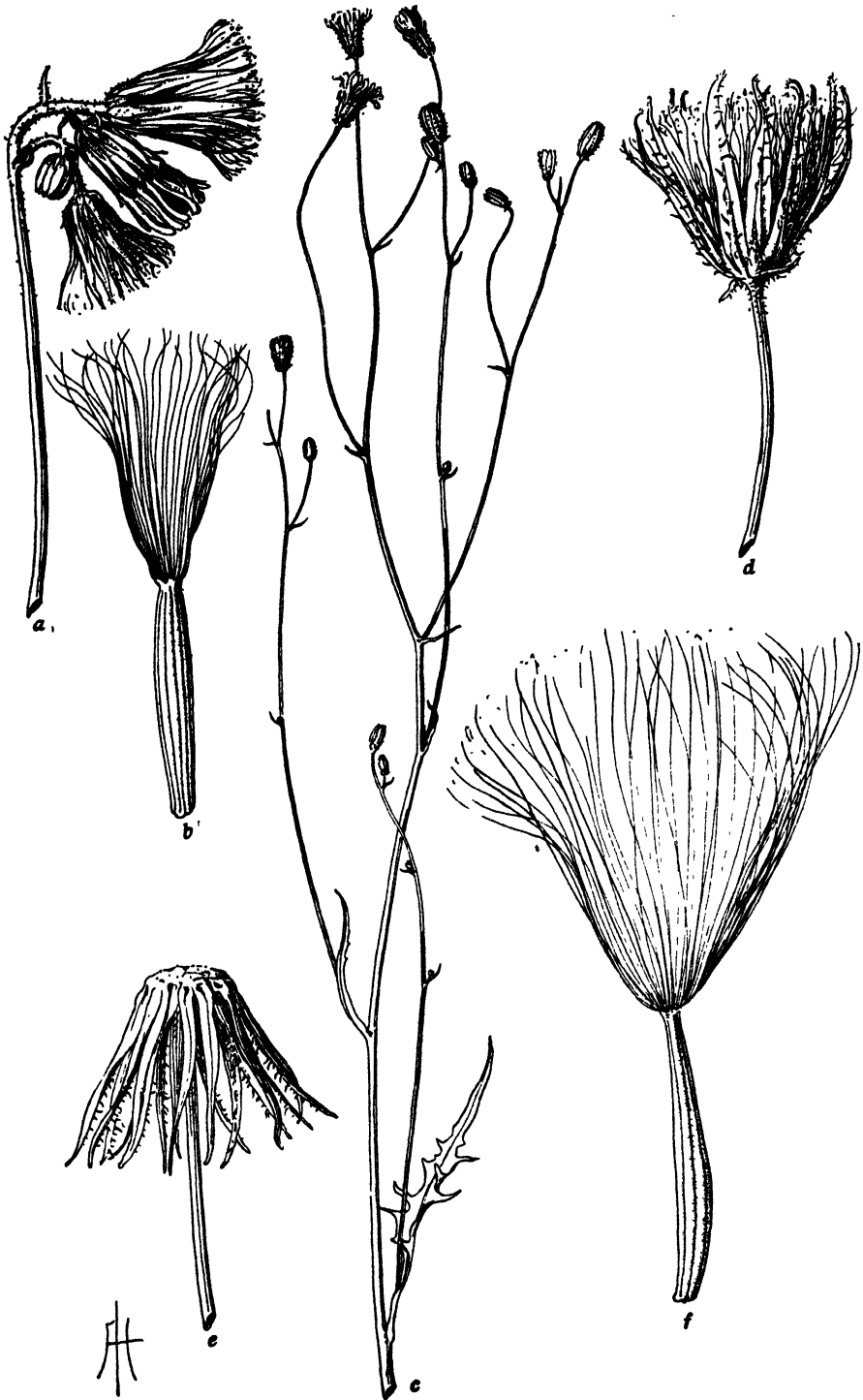


Fig. 200. *Crepis Reuteriana typica*, 2 minor variants, *a*, *b*, from Bornmüller 12096 (Weimar, as var. *aggregata*); *c*–*f*, from Zohary in 1931 (UC 466627, 466649): *a*, part of inflorescence, $\times 2$; *b*, achene with pappus, $\times 8$; *c*, upper part of plant, $\times \frac{1}{2}$; *d*, fruiting head, $\times 2$; *e*, old head, $\times 2$; *f*, achene with pappus, $\times 8$.

midrib beneath, usually pinnately lobed, the lateral lobes \pm retrorse, terminal lobe triangular-truncate to ovate; peduncles 1–10 cm long, glabrous or canescent-tomentulose near the head; heads 20–40-flowered; involucre 10–13 mm long, 4–6 mm wide at middle in fruit, glabrous or sparsely pubescent with pale glandless hairs; outer bracts 8–12, longest $\frac{1}{4}$ – $\frac{1}{3}$ as long as inner bracts; inner bracts 13–16; corolla 14–16 mm long; ligule 1.75 mm wide; teeth 0.4–1 mm long; corolla tube 4–5.5 mm long; anther tube (4) 4.5×1.3 mm dis.; appendages 0.8 mm long, oblong, acute; filaments 0.7–1.2 mm longer; style branches about 2 mm long, 0.15 mm wide, dark green; achenes tawny, 4–5 mm long, 0.5 mm wide, more strongly attenuate toward the apex, slightly constricted above the base, about 15-ribbed. Flowering Apr.–Oct. See figs. 199, 200.

Hieraciodes Reuterianum O. Kuntze, Gen. 1: 346. 1891.

Crepis Reuteriana var. *aggregata* Bornm., Beih. Bot. Centralbl. 31(2): 236. 1914.

W. and S. Asia Minor, Syria, N. Palestine, Cyprus; and Corfu, where it probably is adventive. Reported also from Thrace (Markgraf, 853). It is often found at altitudes between 100 and 1200 m; but in N. Syria, Lebanon, and Cyprus it occurs up to 1900 m.

This subspecies is generally uniform. The most notable variants are: (1) Bornmüller's plant no. 12096, which he named var. *aggregata*, and in which the heads are short peduncled and congested but otherwise typical (fig. 200, *a, b*); (2) certain plants from the Alexandretta-Aleppo reg. which have pubescent involucre and heads and achenes slightly larger than usual—see specimens of Eig and Zohary cited below (fig. 200, *c–f*); (3) those plants in the Amanus Mts., on the ascent from Achagi Zarkoun to Karakisie (see below), in which Eig and Zohary found what is apparently a drouth-caused repressed form with densely hispidulous leaves and few small heads.

Turkey: Bithynia, near Brusa, *Pichler* in 1874 (B); Bithynia, Sabandja, *Endlicher* 64 (B); Lydia, Smyrna, mountains above Sielar, *Boissier* in 1842 (Bo) type; Smyrna, slopes to the east of Koukouloudja, *Balansa* 255 (B); Cilicia, near Mersina, Guzel-Dêré gorge, *Balansa* in 1855 (Bo); Cilicia, Pyramus R., Mt. Nur, *Kotschy* in 1859 (Bo); Cilicia-Kurdistan, Dülük-Baba, near Aintab, *Haradjian* 1191 (DL); Cilicia-Kurdistan, Biredjik (= Birecik), Tat-Sin, *Sintenis* 345 (B); Tscharmelik, *Haussknecht* in 1865 (B, Bo). **Syria:** Amanus Range, Mt. Dûmanly, 700–1200 m, *Haradjian* 3725 (DL); Amanus, near Beilan, *Kotschy* in 1862 (Bo); Amanus, ascent from Achagi Zarkoun to Karakisie, with *Pinus halepense*, *Eig and Zohary* in 1932 (HU); Amanus, between Achagi Zarkoun and Bakajak, *Eig and Zohary* in 1932 (HU); Antioch, environs, *Zohary* in 1931 (UC); Aleppo dist., around Riha, *Zohary* in 1931 (UC); *ibid.*, *Zohary* in 1931 (UC); Alexandretta, around Soukluk, *Zohary* in 1931 (UC); Hammah (= Hama †), *Haradjian* 2567 (DL), an unusually robust plant; Lebanon (Liban), environs of Ehden, 1450–1900 m, *Eig and Zohary* in 1931 (UC); Lebanon, east of Saïda, below Baramie, *Gaillardet* 1360 (US); *ibid.*, *Gaillardet* 2035b (Bo); Mt. Lebanon, Wadi Hammana, *Bornmüller* 12096 (Weimar). **Palestine:** upper Galilee, Dschebel Dscherhan, *Eig* in 1925 (HU); Hebron, in 1926 (UC). **Cyprus:** Komi Kebir, *Haradjian* 302 (DL); Mt. Troodos, *Haradjian* 437, 457 (DL). **Corfu:** without locality, ex hort. genet. Calif. 28.2134–2, grown from seeds received from *J. Sordina* in 1927 (UC).

136, *b. Crepis Reuteriana Eigiana* Babc., Univ. Calif. Publ. Bot. 19: 402. 1941. Stems 0.8–5.5 dm high; caudex elongated, or strongly branched, swollen and sometimes bearing strong fibers at crown; caudical leaves pubescent with pale glandular and glandless hairs evenly spread or denser on midrib and blade, usually coarsely repand-dentate, sometimes pinnatifid with opposite horizontal lateral segments; peduncles 3–18 cm long, gland-pubescent; heads about 20-flowered; involucre 8–13 mm long, 3–6 mm wide at middle in fruit, densely and shortly gland-pubescent, or glabrous; outer bracts 8–10, longest $\frac{1}{4}$ – $\frac{1}{3}$ as long as inner bracts; inner bracts 10–13; corolla about 15 mm long in vigorous plants, shorter in reduced forms;



Fig. 201. *Crepis Reuteriana Eigiana*, a-c, from type (UC 466625); f-h, from Zohary in 1931 (UC 466630); k-m, from hort. genet. Calif. 32.3142 (UC 466629); n, from hort. genet. Calif. 3138 (part of type collection): a, plant, $\times \frac{1}{2}$; b, mature head, $\times 2$; c-e, 3 achenes, 1 with pappus attached, $\times 8$; f, floret lacking ovary, $\times 4$; f', detail of ligule teeth, $\times 25$; g, anther tube, $\times 8$; h, detail of appendages, $\times 32$; k-m, a leaf from each of 3 cultivated plants, k, l, upper face, m, lower face (the last was more completely covered with hairs than is shown here), $\times \frac{1}{2}$; n, somatic chromosomes, $n = 4$, $\times 1250$.

ligules up to 2.5 mm wide; teeth 0.25–0.75 mm long; corolla tube about 4 mm long; anther tube up to 4.5×1.5 mm dis.; appendages 0.8 mm long, oblong, truncate or obtuse; filaments 0.5 mm longer; style branches up to 1.8 mm long, 0.2 mm wide, yellow; achenes greenish-yellow, 5–7 mm long, 1–1.25 mm wide, about equally attenuate to both ends, 15–20-ribbed. Flowering July–Sept. See fig. 201.

Crepis Reuteriana var. *alpina* Boiss., Fl. Orient. 3: 846. 1875.

Mountains of N. Liban, N.W. Syria, and Cilicia. In Lebanon this subspecies occurs between 1500 and 2890 m alt. In the Amanus Range, N.W. Syria, collections have been made between 700 and 1969 m. There has been one collection in the Cilician Taurus at 800 m.

Syria: N. Lebanon, *Cedrus* forest above Bsherre, 1880 m, *Eig and Zohary* in 1931 (UC) type; Liban, Djebel Baruck, *Boissier* in 1846 (Bo) type of var. *alpina* Boiss.; Bsherre, among cedars, *Kotschy* 347 (Bo, MW, B); environs of Ehden, *Lamke* (?) 3505 (Bo); Mt. Hermon, 1600 m, *Eig* in 1924 (HU); between Bakafra and the *Cedrus* forest of Bsherre, *Zohary* in 1931 (UC); *Cedrus* forest above Ehden, *Zohary* in 1931 (UC); Talieh, above the forest of Ehden, *Eig and Zohary* in 1931 (UC); near Talieh, along ditches, *Eig and Zohary* in 1931 (UC); mountains between forest of Ehden and Talieh, 2050–2100 m, *Eig and Zohary* in 1931 (UC); mountains between Ehden and Karneth es Souda, 2100–2500 m, *Eig and Zohary* in 1931 (UC); Karneth es Souda, border of snow fields, 2890 m, *Eig and Zohary* in 1931 (UC); Amanus Range, Mt. Dumanly, 700–1200 m, *Haradjian* 3786 (K); Amanus, Kusliji Dag, 1515–1969 m, *Haradjian* 2502 (K, DL). **Turkey:** Cilicia, Taurus Range, Bozanti hills, about 800 m, *Eig and Zohary* in 1931 (UC).

This subspecies is also fairly uniform, although reduced forms occur, such as *Eig and Zohary's* plant, collected in 1931 between the forest of Ehden and Talieh at 2050–2100 m. This specimen has glabrous stems, peduncles, and involucre, and may be an intergrade between the subspecies. Plants which are certainly intermediate between the subspecies were collected by *Haradjian*, nos. 2502 and 3786, in the Amanus Mts. In these the involucre is glabrous, the caudical leaves short and lyrate-pinnately parted, the style branches yellow, and the achenes larger than in subsp. *typica*.

Relationship

Crepis Reuteriana is closest to *C. pulchra* and *C. palaestina*, but is very distinct from both species in the strong perennial root, the pubescence of the involucre, and in other characters. Artificial hybrids between *C. Reuteriana typica* and *C. pulchra typica* were vigorous but only 3–4 per cent fertile. Second generation progeny were not tested. *C. Reuteriana* exhibits sufficient resemblance to *C. bupleurifolia* of sec. 10 to suggest a phylogenetic connection between the two. The achenes of *C. Reuteriana Eigiana* approach those of *C. bupleurifolia* in size, but there is no indication of the five primary costae which are peculiar to *C. bupleurifolia*.

137. *Crepis palaestina* (Boiss.) Bornm.

Beih. Bot. Centralbl. 31(2): 236. 1914. (Figs. 202, 203.)

Annual, 3–8 dm high; caudex short, narrow in small plants to broad in robust specimens; caudical leaves 10–20 cm long, 3–5 cm wide, oblanceolate, obtuse or sub-acute, lyrate-pinnatifid, terminal segment large, oblong-cordate to reniform, lateral lobes triangular, acute, or lyrate-pinnately parted with large terminal lobe, very narrow rachis and few lateral lobes, the lowest lateral lobes, near the broadened base of the petiole, small and triangular, pubescent on both sides with fine pale glandless hairs; cauline leaves numerous, lowest similar to the caudical, middle ones mostly lanceolate, acute, runcinate-pinnatifid, sessile, broadly auriculate, upper ones linear or bractlike; stem erect, terete, striate, \pm pubescent near base with pale yellow glandless hairs, very shortly gland-pubescent above, paniculately branched

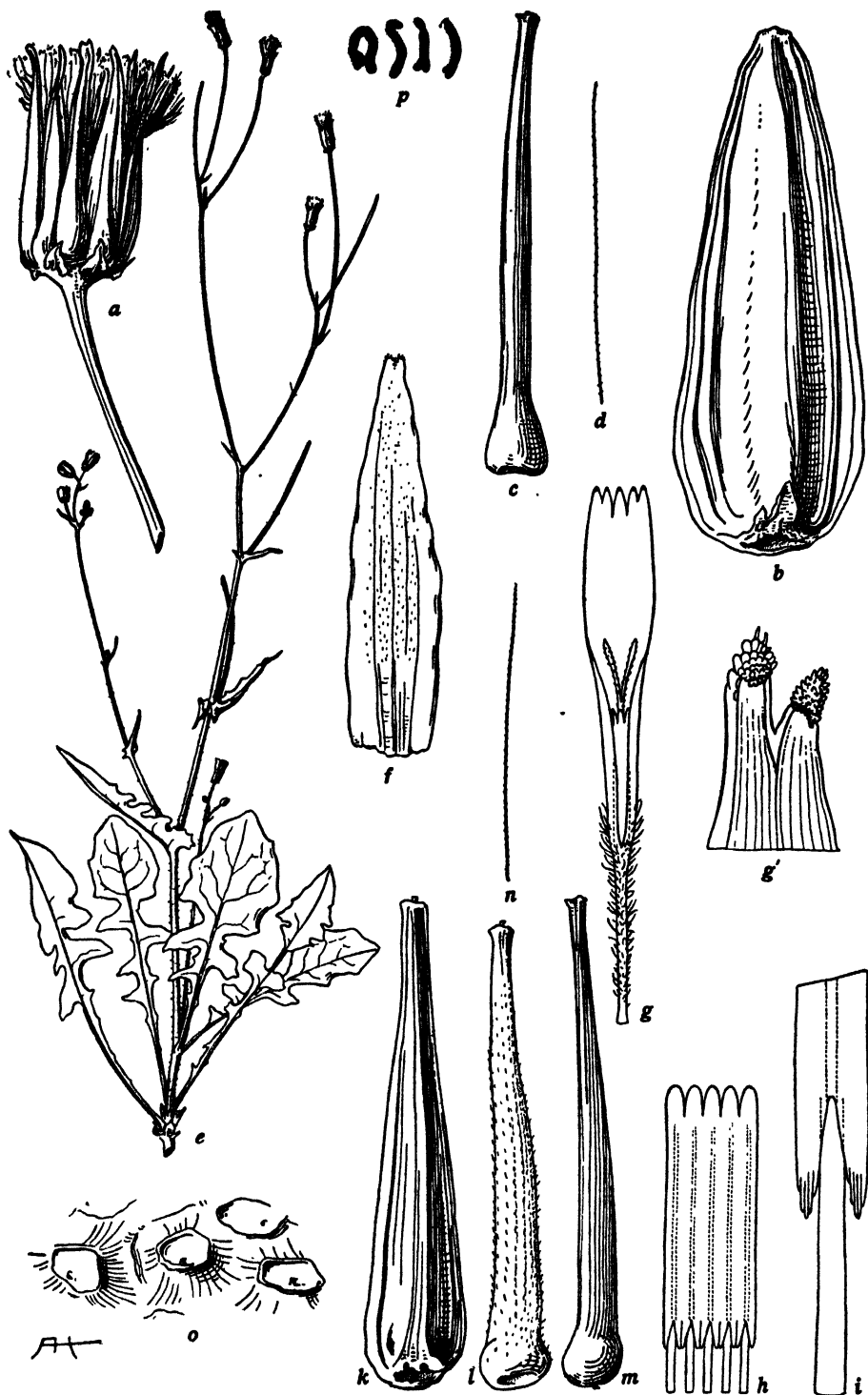


Fig. 202. *Crepis palaestina*, a-f, from type and isotypes, Boissier in 1846 (Bo); g-p, from hort. genet. Calif. 1552 (UC 639626): a, fruiting head, $\times 2$; b-d, marginal and inner achene and pappus seta, $\times 8$; e, plant, $\times \frac{1}{4}$; f, inner involucre bract, $\times 4$; g, floret lacking ovary, $\times 4$; g', detail of ligule teeth, $\times 25$; h, anther tube, $\times 8$; i, detail of appendages, $\times 32$; k-n, marginal, pubescent, and smooth inner achenes and a pappus seta, $\times 8$; o, detail of receptacle, $\times 25$; p, somatic chromosomes, $n = 4$, $\times 1250$.

from below middle, branches remote, strict, gland-pubescent, the lower ones elongated, aggregate inflorescence a many-headed compound corymbiform cyme; peduncles 1–15 cm long, strict or arcuate, longer ones sometimes gland-pubescent below, glabrous above, swollen near base of fruiting heads; heads erect, medium, 25–65-flowered; involucre cylindric, 12–16 mm long, 5–8 mm wide at middle in mature heads, dark green, becoming stramineous and indurate in fruit, glabrous or the bracts \pm pubescent with pale glandless hairs; outer bracts 8–10, about equal, $\frac{1}{5}$ – $\frac{1}{4}$ as long as the inner, ovate, acute, pale-margined; inner bracts 9–13, lanceolate, acute, appressed-pubescent on inner face, becoming very prominently carinate dorsally and pale spongy-thickened confluent with the base; receptacle areolate, glabrous; corolla 15–19 mm long; ligule 2.25–2.5 mm wide; teeth 0.4–1 mm long; corolla tube 5–6.5 mm long, densely pubescent with several-celled contorted hairs; anther tube (3.25)5 \times 1.3 (1.6) mm dis., yellow, tinged green at summit; appendages 0.5–0.7 mm long, lanceolate, acute; filaments 0.5–0.8 mm longer; style branches 1.4–2.25 mm long, 0.1–0.15 mm wide, dark green; achenes mostly tawny or light brown, 6–10 mm long, biform; marginal achenes usually bald or the pappus early deciduous, \pm obcompressed and laterally alate, but extremely variable, ranging from 1 to 3 mm wide in different forms of the species, and sometimes only 1 or 2 per head; inner achenes terete, gradually attenuate upward, with slightly expanded pappus disk, conspicuously dilated at the hollow base, weakly or definitely 15–20-striate, striae glabrous, or in some forms (cf. m.v. 1) some of the inner achenes densely spiculate; pappus white, 4.5–6 mm long, multiseriate, extremely fine, soft, flexuous, persistent or deciduous. Flowering Apr.–May; flowers yellow. Chromosomes, $2n = 8$.

Cymboseric palaestina Boiss., Diagn. Ser. I, 11: 51. 1849.

W. Syria from the region of Latakiah southward to Saida, in low littoral situations and in mountains, especially Liban and the valley to the east; Palestine, near Haifa, on Mt. Carmel, Mt. Tabor, in Samaria, vicinity of Jerusalem, etc.; Cyprus. Reported by Boissier (830) to occur in woods in Syria as well as near the sea (in the spring) and on Cyprus in bogs. Acc. to Post (152), this plant is found in shady places.

The type, cited below, is in herb. Boiss., Genève.

Although Boissier erected a new genus for this species on the basis of the peculiarly shaped achenes, Bentham and Hooker merged the genus with sec. *Phaegasium*, along with *C. pulchra* and *C. Reuteriana*; and Hoffman (E. and P.) reduced the genus to a section next to *Phaegasium*. Bentham and Hooker even stated that *Cymboseric* "is not easily distinguished from large-flowered oriental specimens of *C. pulchra*." But, as mentioned by Holmboe (Berg. Mus. Skrifter, Ny Raekke B. 1(2): 195. 1914), *C. palaestina* is always easily distinguished by the shape of the fruits. When mature achenes are lacking, the leaf shape, head size, and number of florets per head may be used to distinguish them. *C. palaestina* has lyrate basal leaves with a large terminal lobe; *C. pulchra* has the basal leaves denticulate to runcinate-pinnatifid (very rarely sublyrate). In *C. palaestina* the mature involucre is 12–16 mm long; in *C. pulchra* they are 8–11 (rarely 12) mm long and correspondingly narrower. In *C. palaestina* the heads are 25–65-flowered; in *C. pulchra*, 15–30-flowered. In *C. palaestina*, also, the florets are usually much larger than in *C. pulchra*; and the anther tubes are more green than yellow and often entirely green. There is some overlapping of these characteristics in the two species, but the shape of the basal leaves alone will usually serve to distinguish them.

In *C. palaestina* there exists considerable variation, especially in its most important distinguishing feature, the achenes. The type and isotypes (in herb. Boiss.),

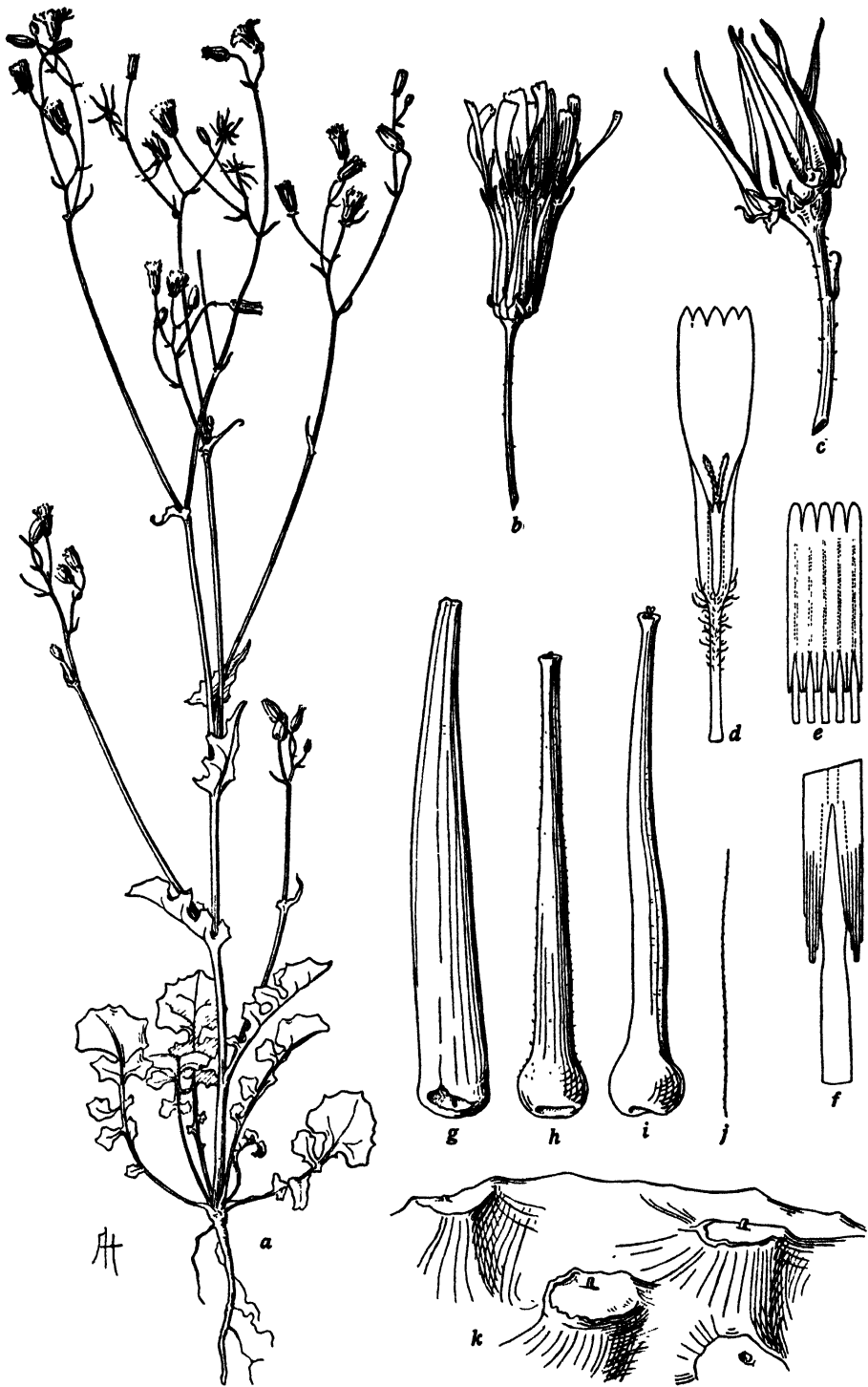


Fig. 203. *Crepis palaestina*, m.v. 2, a, from Gaillardet 2434 (Bo); b-k, from hort. genet. Calif. 3156 (UC 639625): a, plant, $\times \frac{1}{4}$; b, flowering head, $\times 2$; c, fruiting head, $\times 2$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g-j, marginal, pubescent, and smooth inner achenes and a pappus seta, $\times 8$; k, detail of receptacle, $\times 25$.

collected on Mt. Tabor in Palestine, have extremely wide (very broadly winged) marginal achenes and the inner achenes are all glabrous (fig. 202, *b, c*). In most plants the marginal achenes are definitely but less broadly winged, being more like those in fig. 202, *k*. In many plants, as in m.v. 1, some of the inner achenes are densely spiculate (fig. 202, *l*). Plants of this variant have been collected in the same situation with plants of the typical form; it is highly probable that a comparatively simple genetic difference is responsible for the two forms. Another extreme variation in the marginal achenes was discovered in a collection from N. Liban (see m.v. 2); but in this the lateral wings of the marginal achenes are almost lacking (fig. 203, *g*). The cultivated progeny, however, were variable in this respect. Under cultivation, in fact, this species has proved to be more or less variable in length of growing period or time of maturity, in depth of yellow color of the ligules, in leaf width and shape of lobes, in thickness and texture of the leaves, in amount of pubescence, and in degree of bitterness when the leaf is chewed. But many of these potential variations are probably repressed under natural conditions.

Syria: Musairy Mts., Bahenna, about 30 km east of Ladikije (Latakiah), about 300 m, *Haradjian 2941* (DL); *ibid.*, *Haradjian 2857* (DL) m.v. 1; Beirut, *Gaillardet 987* (Bo); Beirut, *Kotschy 328* (UWM) m.v. 1; Ras-Beirut, wasteland, *Bornmüller 12085* (UWM); Beirut, *Barbey 572* (B); Saida, Mar Elia, fields, *Gaillardet 2433* (Bo); Saida, enclosed garden, *Gaillardet 2434* (Bo) m.v. 1; *ibid.*, *Gaillardet 4102* (Bo) m.v. 1; Liban, environs of Ehden, banks of ditches, about 1750 m, *Eig and Zohary* in 1931 (UC) m.v. 2; Liban, east of Ghazir, calcareous rocks, *Gaillardet 2760b* (Bo). **Palestine:** Mt. Tabor, *Boissier* in 1846 (Bo, *b* = type, UCf); Samaria, *Boissier* in 1846 (Bo); Samaria, hills, *J. Ball 1221* (Bo) m.v. 1.

Minor Variants of C. palaestina

1. Some of the inner achenes densely spiculate. This variation occurs in the same populations with typical forms which have all the inner achenes glabrous. (Fig. 202, *k-m*.) *Haradjian 2857* (DL) Bahenna, near Latakiah, Syria; *Kotschy 328* (UWM) Beirut, Syria; *Gaillardet 2434, 4102b* (Bo, UCf) Saida, Syria; *J. Ball 1221* (Bo) hills of Samaria, Palestine.

2. Inner achenes as in m.v. 1 and marginal achenes narrow, whitish, subterete, glabrous, obscurely alate near base, gradually attenuate to the very narrow summit, $\frac{1}{4}$ – $\frac{1}{3}$ longer than inner achenes; pappus 3–4 mm long. The progeny of the original wild plant were variable with respect to width of the marginal achenes. (Fig. 203.) *Eig and Zohary* in 1931 (UC), banks of ditches, environs of Ehden, N. Liban, Syria.

Relationship

Crepis palaestina may be considered the most primitive of the annual species in this section on the basis of the lyrate basal leaves and the larger size of the flower heads, flowers, and fruits. Although it is very distinct from its nearest relative, *C. pulchra*, in shape of the basal leaves and size of the heads, flowers, and fruits, as well as the peculiarly shaped achenes, it is actually very close to *C. pulchra* genetically. This is indicated by the fact that, on the basis of seed-setting under open-pollination, F_1 hybrids between the two were 30–50 per cent fertile. Also, the F_2 progeny were vigorous and more or less fertile. So far as known, however, the two species never hybridize in nature. Either they do not occur in the same situations or, when they do occur together, they flower at different times. Field studies are needed in order to establish these points beyond question. But it may be noted that *C. pulchra* usually occurs in open situations, whereas *C. palaestina* seems to be a "shade-loving" species. Furthermore, the geographic areas of the two overlap only near the northern limit of *C. palaestina*. Hence, they are nearly isolated geographically and, in the overlapping region, they are apparently isolated ecologically as well as by the difference in time of flowering (see Part I, p. 150).

138. *Crepis pulchra* L.

Sp. Pl. 2: 806. 1753. (Figs. 204–207.)

Annual, 0.5–10 (mostly 3–7) dm high; root slender, vertical; caudex narrow, leafy; caudical leaves rosulate, 1–24 (mostly 3–15) cm long, 0.5–5 (mostly 1–3) cm wide, oblanceolate, acute or obtuse, denticulate to runcinately dentate or pinnatifid with triangular acute lobes, attenuate into a narrowly winged petiole, pubescent on both sides with pale hairs which are short and glandular or longer and glandless or both intermixed; lower cauline leaves similar, the middle ones lanceolate, acute or acuminate, denticulate to subpinnatifid, sessile, subamplexicaul, pubescent, the uppermost linear or bractlike; stem erect, sulcate or striate, fistulose, densely pubescent near base with pale glandless and shorter glandular hairs, often glabrescent above, cymosely branched, sometimes near the summit, sometimes from the base upwards, or from the mid-region, lower branches elongated, making a compound corymbiform aggregate inflorescence; peduncles 1–4.5 cm long (sometimes 6–9 mm in reduced specimens), slender, glabrous, somewhat thickened near fruiting heads; heads erect, small, 15–30-flowered; involucre cylindric in anthesis, turbinate in fruit, 8–11 (12) mm long, 3–5 mm wide at middle in fruit, glabrous; outer bracts 5–7, very short, ovate or lanceolate, acute or acuminate, pale membranous-margined; inner bracts 12–14, lanceolate, acute, glabrous on inner face, in anthesis with yellow median dorsal nerve, in fruit becoming strongly carinate and pale spongy-thickened confluent with the base, ultimately reflexed; receptacle glabrous; corolla 5–12 mm long; corolla tube densely pubescent with fine many-celled tortuous hairs; anther tube 1.5–4 mm long; style branches 0.75–1.5 mm long, dark green, greenish, or yellow; achenes bifiform or (subsp. *typica*) sometimes uniform; marginal achenes 5–6 mm long, \pm obcompressed, \pm attenuate, usually without pappus; inner achenes 4–4.5 (5) mm long, terete, \pm attenuate, bearing copious pappus, outermost spiculate, inner ones weakly striate; pappus dusky or pure white, 3–5 mm long, mostly 4–5-seriate, very fine, soft, rather persistent. Flowering Apr.–Aug.; flowers light yellow.

Mediterranean reg., middle Europe, and eastward to the W. Himalaya and Tien Shan mts. Dry situations at various elevations ranging from near sea level to 3000 m.

This well-known distinctive species is fairly uniform throughout its wide range in habit and leaf shape as well as in involueral and achenial characters. But critical study of comparative morphology, supplemented by observations on many cultivated strains, has demonstrated the existence of 3 subspecies.

Key to the Subspecies of Crepis pulchra

Florets mostly smaller; corolla 5–9 (11) mm long; anther tube 1.5–2.5 mm long; flower heads closing before noon. 138, *a. typica*

Florets mostly larger; corolla 10–12 mm long; anther tube 3–4 mm long; flower heads remaining open most of the day.

Ligules purple on outer face; achenes coarser, 0.5–0.7 mm wide. 138, *b. africana*

Ligules lacking purple; achenes finer, 0.3–0.5 mm wide. 138, *c. turkestanica*

138, *a. Crepis pulchra typica* Bab., Univ. Calif. Publ. Bot. 19: 402. 1941. Flower heads less conspicuous, always closing before midday and often earlier; corolla 5–11, mostly 6–9 mm long; ligule 1.2–1.5 mm wide; teeth 0.1–0.25 mm long; corolla tube about 4 mm long; anther tube 2.5 \times 1 mm dis., yellow below, greenish above; appendages 0.4–0.5 mm long, narrow, acute, or obtuse; filaments 0.3–0.75 mm longer; style branches 0.75–1 mm long, 0.1 mm wide, dark green; achenes either all terete and then the marginal ones spiculate, or the marginal obcompressed and usually

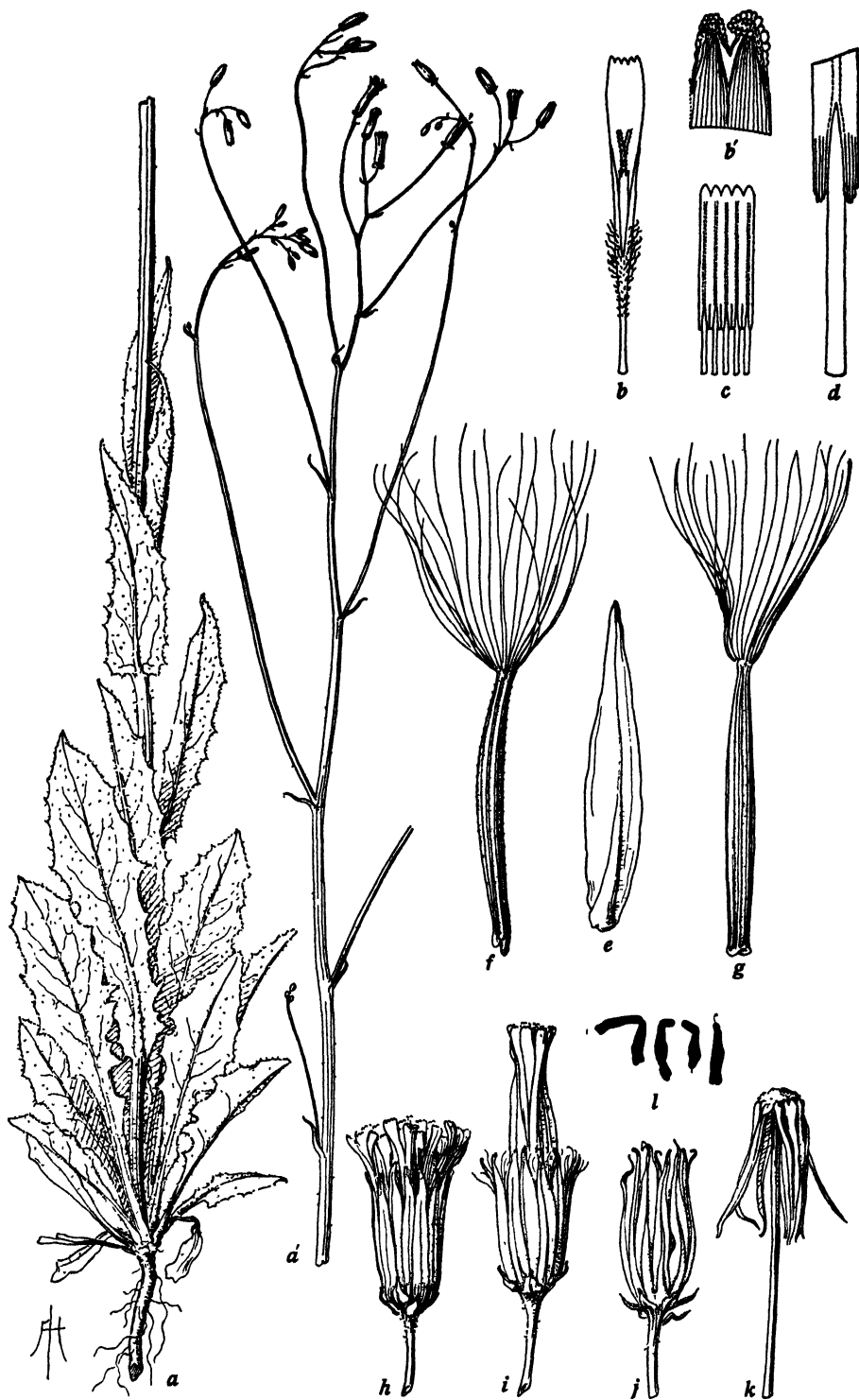


Fig. 204. *Crepis pulchra typica*, a-g, from Fourès in 1903 (UC 669407); h-l, from hort. genet. Calif. 29.1483-2 (UC 669376): a, plant, $\times \frac{1}{2}$; b, floret lacking ovary, $\times 4$; b', detail of ligule teeth, $\times 50$; c, anther tube, $\times 8$; d, detail of appendages, $\times 32$; e, inner involucre bract, outer face, $\times 4$; f, marginal achene with pappus, $\times 8$; g, inner achene with pappus, $\times 8$; h-k, heads, $\times 2$; l, somatic chromosomes, $n = 4$, $\times 1250$.

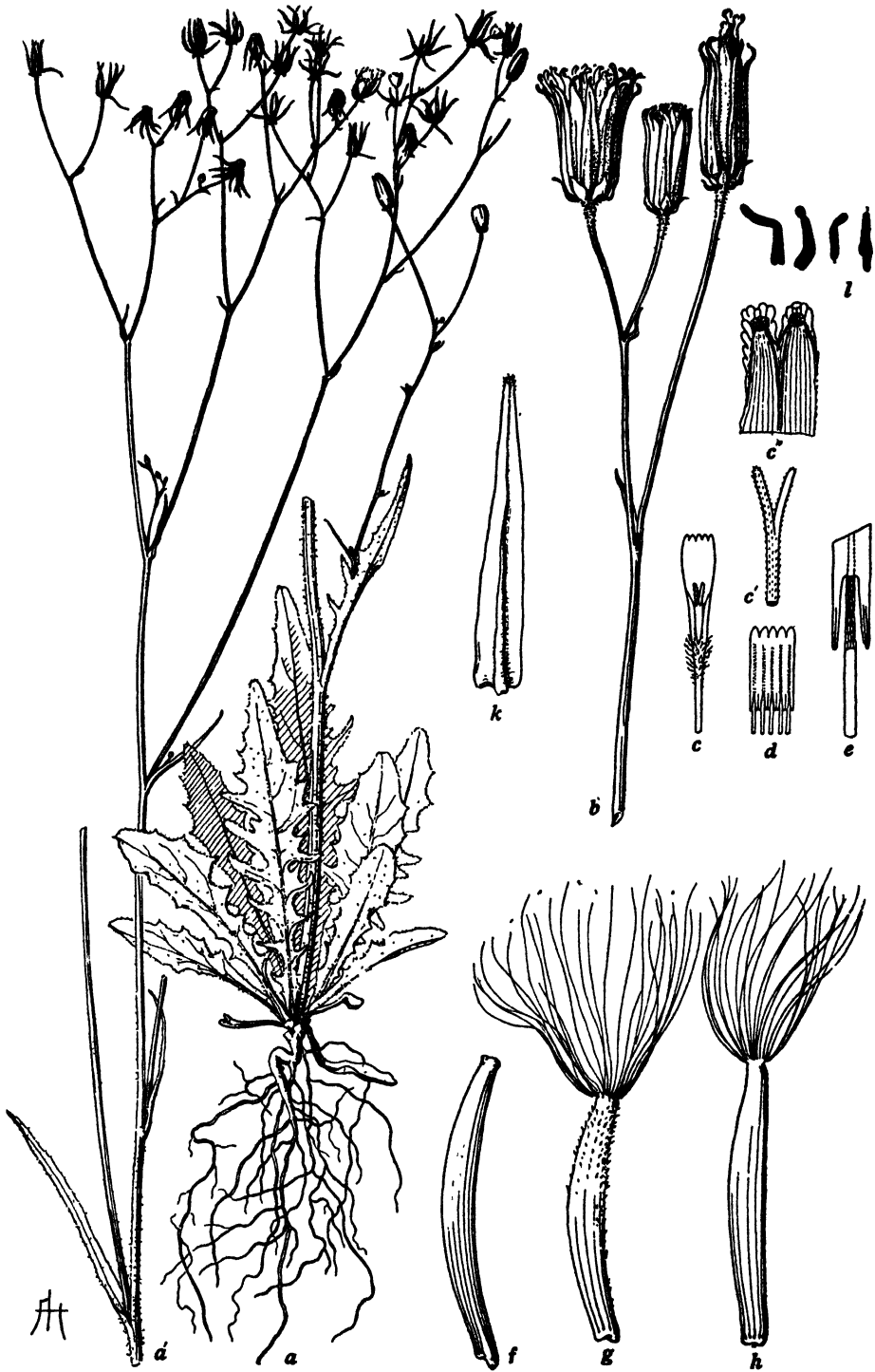


Fig. 205. *Crepis pulchra typica*, m.v. 1, from a plant grown from seed collected in Spain, Sierra Nevada, by Maire in 1926, hort. genet. Calif. 28.1894-1 (UC 531845); a, a', plant, $\times \frac{1}{2}$; b, young heads, $\times 2$; c, floret lacking ovary, $\times 4$; c', style branches, $\times 12.5$; c'', ligule teeth, $\times 50$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, marginal achene, $\times 8$; g, h, inner achenes, $\times 8$; k, inner involucre bract, $\times 4$; l, somatic chromosomes, $n = 4$, $\times 1250$.

lacking pappus, the inner ones terete and of these the outermost spiculate, the others smooth and weakly striate; pappus dusky white, 4–5 mm long. Chromosomes, $2n = 8$. See figs. 204, 205.

Crepis pulchra L., Sp. Pl. 806. 1753.

Chondrilla pulchra Lamk., Fl. Fr. 2: 106. 1778.

Lampsana pulchra Vill., Hist. Pl. Dauph. 3: 163. 1789.

Prenanthes paniculata Moench, Meth. 534. 1794.

Prenanthes hieracifolia Willd., Sp. Pl. 3: 1541. 1800.

Prenanthes pulchra DC., Fl. Fr. 4: 7. 1805.

Prenanthes viscosa Baumg., Enum. Stirp. Transylv. 3: 44. 1816.

Phaeacasium lampsanoides Cass., Diet. 39: 387. 1826.

Idianthes pulchra Desv., Fl. Anj. 199. 1827.

Sclerophyllum pulchrum Gaud., Fl. Helv. 5: 48. 1829.

Intybellia pulchra Monn., Ess. Hierac. 79. 1829.

Crepis youngiformis Koch, Linnaea 17: 277. 1843.

Youngia Kochiana Ledeb., Fl. Ros. 2: 837. 1844–1846.

Phaeacasium pulchrum Benth. et Hook., Gen. Pl. 2: 516. 1873.

Crepis hispanica Pau, Not. Bot. Fl. Hispan. 1: 11. 1887 et 11: 30. 1889.

Crepis cylindrica St.-Lager, ex Cariot, Etud. Fl. ed. 8, 2: 500. 1889.

Hieraciodes pulchrum O. Kuntze, Gen. 1: 346. 1891.

Crepis valentina Willk., Suppl. Fl. Hisp. 116. 1893.

Crepis pulcherrima Grossheim, Act. Hort. Tiflis, ser. 2, 1: 145. 1920.

Most of Spain, France, S.W. Germany, Switzerland, N. Italy, the Balkan states and northward to Czechoslovakia, S. Russia, Caucasus, and Asia Minor, and in Syria acc. to Post (154).

Comprising the major part of the species, this subspecies includes forms with uniform or biform achenes. When the achenes are biform the obcompressed marginal ones usually bear no pappus. Since the type specimen of *Linnaeus* has terete achenes and none without pappus, uniform achenes must be considered typical of this subspecies. At the same time, plants with biform achenes occur generally throughout the range of the subspecies; and the other two subspecies both have biform achenes. Furthermore, the closely related *C. palaestina* has similar obcompressed marginal achenes, but these are occasionally reduced in number to only one or two. Therefore, plants of *C. pulchra* lacking obcompressed marginal achenes may be considered as reduced forms. They certainly appear sporadically throughout the range of this subspecies, and they may be due to a recurrent gene mutation.

Spain: Teruel Prov., Origuella, *Reverchon* (UC, Grenoble) as *C. valentina*; Valencia Prov., Sierra de El Toro, *Pau* (Bar) as *C. hispanica*; Alicante Prov., Aitana Mts., near Alcoy, *Font Quer* in 1923 (Bar); Malaga Prov., Ronda, *J. Ball* in 1851 (US); Granada, *Winkler* (Po); Jaen Prov., Barranca de Valentina, *Reverchon* in 1904 (Ms); Catalonia, Monreal del Campo, *Benedicto* in 1894 (Bar) as *C. valentina fide Pau*; Catalonia, Barcelona, Triadabo, *Valldaura*, *Sennen 3724* (Bar, Bur); Sierra Nevada, Geuil Valley, cult. from seeds collected by R. Maire in 1926 (UC) m.v. 1; N.E. Cadiz Prov., Sierra del Pinar, 1200 m, *Font Quer* in 1925 (Bar, UC) m.v. 1. **Morocco:** Djebel Zerka, *Gandoger* in 1909 (Mo); Djebel Lexhab, up to 2000 m, *Font Quer* in 1930 (UC). **France:** Aveyron Prov., *Fourès* in 1903 (UC); environs of Paris, *Jeanpert* in 1876 (Minn); Meuse Prov., Verdun, *Bullemont 3311* (Bur, Ms); Vendée Prov., Gachet, *Ayrand* in 1855 (Bur); Cote d'Or Prov., Gevrey-Chambertin, *Hall 12407* (UC); Aubagne, near Marseille, *Hall 12495* (UC); Var Prov., near Hyères, *Raine* in 1909 (G); Alpes Maritimes, St. Etienne de Tinée, 1400 m, *St. Yves* in 1914 (Bur); Alpes Maritimes, La Briga, *Burnat* in 1872 (Bur); Isère Prov., near Grenoble, *Pellat* in 1887 (Minn); Hautes Alpes, Monétier-les-Bains, 1500 m, *Faure* in 1924 (UC). **Italy:** Lombardy, Alpes Bergomasques, *Rodegher* (DL); Piemont, St. Bernard, *Meroier* in 1845 (DL); *ibid.*, between St. Bernard and Aosta, *Muret* (Bur); Verona, between Torri and Caprino, *Burnat* in 1873 (Bur). **Switzerland:** Valais, above Etroubles, route du St. Bernard, *Fauconnet* (DL) with critical notes by Rapin in 1852. **Germany:** Rheinland, near Luxembourg, *Dürer* in 1886 (Minn); near Meisenheim, *F. Schultz* (Bur). **Hungary:** Ofen, Blocksberg, *Bohatsch* in 1876 (DS); *ibid.*, Adlersberg, *Bohatsch* in 1879 (Bur); near Budapest, *Simonkai 3412* (Bur, Minn). **Czechoslovakia:** Kovacovske Mts., Skaly, *Domin*, *Krajina et Deyl* in 1929

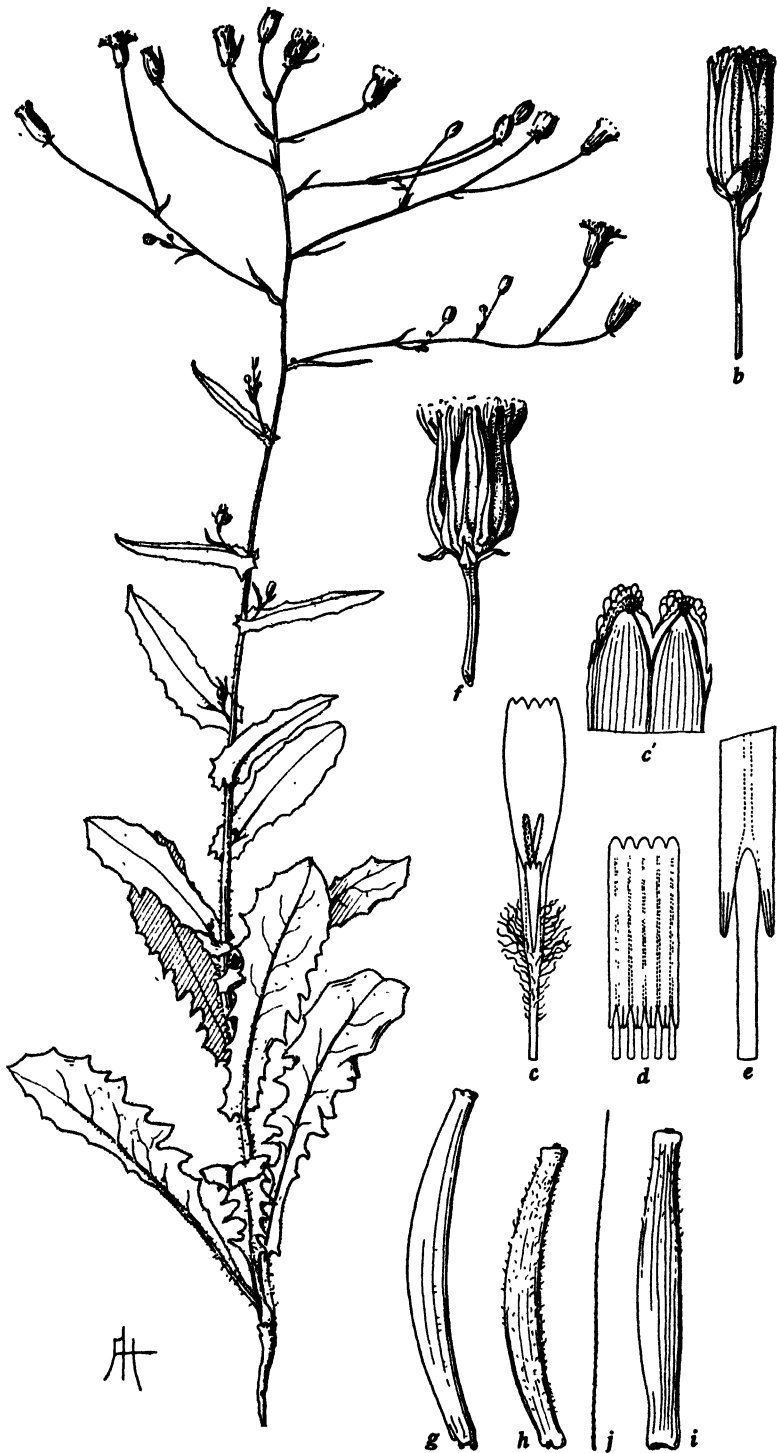


Fig. 206. *Crepis pulchra africana*, from plants grown from seeds collected in Algiers by Maire in 1930, ex hort. genet. Calif., a, f, 31.2963-2 (UC 540728); b-e, 34.2963-5, and g-i, 34.2963-9 (UC 531837): a, plant, $\times \frac{1}{2}$; b, head, $\times 2$; c, floret lacking ovary, $\times 4$; c', ligule teeth, $\times 50$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, fruiting head, $\times 2$; g, marginal achene, $\times 8$; h-j, inner achenes and a pappus seta, $\times 8$.



Fig. 207. *Crepis pulchra turkestanica*, a-f, from hort. genet. Calif. 34.2566-6 (UC 540726); g-k, from 29.2566-4 (UC 531830): a, basal leaf, $\times \frac{1}{2}$; b, caule leaf, $\times \frac{1}{2}$; c, aggregate inflorescence, $\times \frac{1}{2}$; d, floret lacking ovary, $\times 4$; d', ligule teeth, $\times 50$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, fruiting head, $\times 2$; h, marginal achene, $\times 8$; i, j, inner achenes, $\times 8$; k, inner involucre bract, outer face, $\times 4$.

(US, G, Mo, UC). **Rumania:** Transylvania, Aloins Mts., *Barth* in 1895 (Bur). **Dalmatia:** without locality, *Boemer* (Mo). **Bulgaria** (*vide* Stefanoff): *Lucovit*, *Urumov* (Sofia); *Sumen*, *Javachev* in 1901 (Sofia-M); *Burgas*, *Stojanoff et Stefanoff* in 1921 (Sofia-M); *Trojan*, *Urumov* (Sofia-M); *Varna* dist., near *Gebedje*, *Besdek* in 1897 (Sofia-M); *Stanimaka*, *Stribrny* in 1894 (Sofia-M); *E. Rhodope Mts.*, above *Mastanli*, *Davidov* in 1914 (Sofia-M). **Thrace** (*vide* Stefanoff): *Kumbaga*, near *Bodosto*, *Nicolov* in 1913 (Sofia-M); *Adrianople* dist., *Karassakli*, *Neiceff* in 1913 (Sofia-M); near *Constantinople*, *Bujuk-han*, *Davidov* in 1913 (Sofia-M). **Greece:** *Thessaly*, *Kalampaka*, *Freyn* 408 (UWH). **Turkey:** western, near *Mudania*, maritime, *Bornmüller* 5221 (UWG, BB); southern, *Konieh*, *Heldreich* 617 (B); southeastern, *Biredjik*, *Sintenis* 527 (K); eastern, *Kurdistan*, *Sintenis* 940 (K). **Syria:** environs of *Hammah*, *Haradjian* 1800 (DL); environs of *Homs*, *Haradjian* 3237 (DL); *Amanus Mts.*, between *Coldrin* and *Bujukaba*, *Eig and Zohary* in 1931 (UC, HU). **Iraq:** "Mesopotamia," *Sintenis* 527 (K). **Persia:** near ruins of *Persepolis*, *Hohenacker* in 1842 (Mo). **U. S. S. R.:** *Caucasus*, *Georgia*, *Wülsen* (DL); *Caucasus*, cult. from seeds received through *M. Navashin* as *C. pulcherrima* (UC).

Minor Variant of C. pulchra typica

1. Corolla very small, only 5.5–7 mm long; anther tube 1.5–1.7 mm long, yellowish-green; style branches 0.75–1.3 mm long, yellow or greenish; achenes biform, the marginal 5.5 mm long, 0.7 mm wide, without pappus; the inner 4.5–5 mm long, 0.7 mm wide; pappus pure white, 3–5 mm long. Chromosomes $2n=8$, identical with those of subsp. *typica*. This form, or a strain of it from the Spanish *Sierra Nevada*, has been cultivated for several years in hort. genet. Calif., under the name of *C. granatensis*, under which name the chromosomes were reported and illustrated (B. and C., 288, 309). But the morphological distinctions between this and other forms of subsp. *typica* are so minute that assignment to a higher category than variant seems hardly warranted. Furthermore, as the specimens cited below show, this same form occurs in more than one locality. (Fig. 205.) *Maire* in 1926 (UC) seeds collected in *Geuil Valley*, *Sierra Nevada*, plants cult. in hort. genet. Calif. 28. 1894–1, 6; *Font Quer* in 1925 (Bar, UC) *Sierra del Pinar*, N.E. *Cadiz Prov.*, Spain.

138, b. *Crepis pulchra africana* Bab., Univ. Calif. Publ. Bot. 19: 402. 1941. Flower heads more conspicuous than in subsp. *typica*, remaining open most of the day; corolla 10–12 mm long; ligule 2 mm wide, reddish-purple on outer face; teeth 0.1–0.3 mm long; corolla tube 3.5 mm long; anther tube 3.2×1 mm dis., dark green above, yellowish at base; appendages 0.4 mm long, lanceolate, acute or acuminate; filaments 0.5 mm longer; style branches 1.25 mm long, 0.1 mm wide, dark green; achenes biform, the marginal obcompressed, 5.5 mm long, 0.5 mm wide, lacking pappus, the inner terete, 4.5 mm long, 0.7 mm wide, and of these the outermost spiculate, the others smooth and weakly striate; pappus white, about 5 mm long. (See fig. 206.)

Known with certainty only from the vicinity of Algiers. In addition to the type locality, cited below, Dr. *Maire* informs me that he has collected this subspecies above the *Jardin d'Essai du Hamma*, which is situated in the hills south of Algiers; but one specimen (in Herb. Missouri Bot. Gard.) collected by *Muschler* in Upper Egypt, near *Luksor*, may be this subspecies. It may be found in Morocco, where subsp. *typica* also occurs.

Algeria: *Alger*, rocks of *Telemly*, *Maire* in 1930 (UC) type; ex hort. genet. Calif. 31. 2963–1, 2, and 5, cult. from seeds collected by Dr. *Maire* in Algeria in 1930 (UC).

138, c. *Crepis pulchra turkestanica* Bab., Univ. Calif. Publ. Bot. 19: 402. 1941. Flower heads, as in the last, more conspicuous than in *typica*, remaining open most of the day; corolla 10–12 mm long, ligule 2.5 mm wide, without red on outer face; teeth 0.3–0.6 mm long; corolla tube 2.5 mm long; anther tube 3.75×1.25 mm dis., dark green; appendages 0.5 mm long, oblong, sagittate, acute; filaments 0.25–0.75 mm longer, the anterior one longer; style branches 1–1.5 mm long, 0.1 mm wide, dark green; achenes biform, narrower than in subsp. *africana*, 0.3–0.5 mm wide, the marginal 5–6 mm long, without pappus, the inner terete, 4–5 mm long,

and of these the outermost spiculate, the others smooth and weakly striate; pappus white, 3–5 mm long. See fig. 207.

Launaea pulchra N. Pav., Fl. Cent. Kazakstan III: 360. 1938.

Crepis carinata Babcock, in herb.

Central and S. Turkestan, Afghanistan, and westward through Persia and Turkey, thus overlapping the area of subsp. *typica*.

Turkestan: ex hort. genet. Calif. 29. 2566–4, cult. from seed collected by Dr. Zaetsev, Taskent Plant Breeding Station (UC) type; Syr-Darja Prov., Tashkent dist., near Tashkent, *Popov et Vvedensky* in 1924 (Mo, NY); Samarkand dist., Pistaly-tan Mts., *Spiridonow* in 1915 (UC); ex hort. genet. Calif. 29. 2370–2, cult. from seeds collected by Dr. Popov in Actau Mts., Samarkand (UC); Turcomania, Aschabad, mountains, *Litwinow* 1416 (G); ex hort. genet. Calif. 34. 2371–3, cult. from seeds collected by Dr. Popov in Zervaschan Valley (UC); Pamir reg., Maili-Tsai, *Kuschakewicz* in 1878 (B, P). **Afghanistan:** Kurrum Valley, *Aitchison* in 1879 (B, G); Kurrum Valley, Shalizan, *Aitchison* 312, Alikhel, *Aitchison* 562 (DD); without locality, *Griffith* 3358 ex herb. East India Co., distributed from Kew, 1862–1863 (Mu, G). **Persia:** ruins of Persepolis, *Kotschy* 255 (Bo, PC, G, Mo); Kuh-Dana Mts., *Kotschy* 691 (Bo); base of Mt. Demawend, *Kotschy* in 1843 (B); Kerman Prov., near Kerman, *Bornmuller* 4141 (B, UWG). **Iraq:** "prope Tigrim," *Kotschy* in 1841 (UWM); Baghdad, *Hausknecht* in 1868 (Bo). **Turkey:** Kurdistan, Mardin, *Stapf* 940 (B, Mu); Malatya, *Balls* 2301 (UC); between Orfa (= Urfa) and Suerek, *Kotschy* in 1843 (Bo); Gulf of Adalia, port of Tekhirova, mines of Phasolis, no. 617 in 1845 (Bo); Smyrna, *Balansa* in 1854 (Bo).

Relationship

Crepis pulchra, the type species of sec. *Phaeccasium*, occupies an intermediate position in the section, standing between *C. palaestina* and *C. pterothecoides*. Like the former, it usually has biform achenes, whereas the latter is more specialized in its shortly beaked, uniform achenes and its relative precocity.

139. *Crepis amanica* sp. nov.

(Fig. 208.)

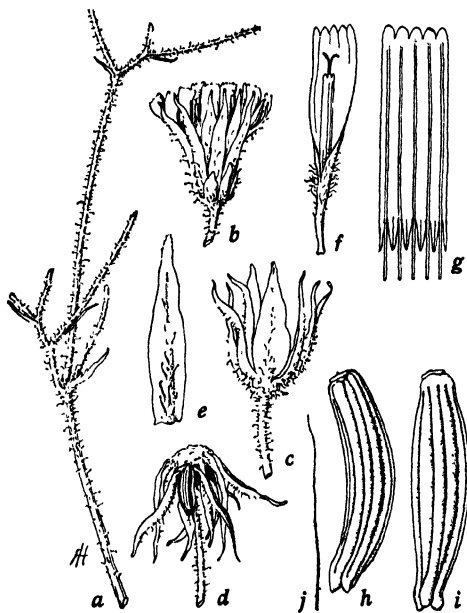


Fig. 208. *Crepis amanica* from type (DL): a, fragment of stem, showing upper cauline leaves and glandular pubescence, $\times 1$; b, head in anthesis, $\times 2$; c, mature involucre, $\times 2$; d, old head, showing naked receptacle, $\times 2$; e, inner involucre bract from mature head, $\times 4$; f, floret lacking ovary, $\times 4$; g, anther tube, $\times 8$; h–j, marginal and inner achenes and a pappus seta, $\times 8$.

Herba annua 5–6 dm alta; caulis erectus crassiusculus viridus striatus hispidulus 3-furcatus; folia caulina amplexicaulia auriculata inferioribus pinatifidis superioribus integris; rami elongati ad summitatem cymose ramulosi subcorymbosi 2–4-cephalici ramulis et pedunculis dense pubescentibus et glandulosis; capitula parva circa 20-flora; involucrem nigro-viridum campanulatum 7–8 mm altum 4–5 mm latum, squamis exterioribus 6–8 parvisimis acuminatis, interioribus 12–15, lanceolatis acutis intimibus late marginatis membranaceis in dorso dense pubescentibus vel setulosis et glandulosis ventrale pubescentibus pilis brevissimis in maturitate incurventibus valde carinatis et spongioso-incrassatis ultimo reflexis; receptaculum areolatum glabrum; corolla circa 6–7 mm longa, ligula 1.5 mm lata ad basim pubescenti, tubo 2–2.5 mm longo dense pubescenti pilis tortuosis; antherae

circa 3 mm longae flavido-viridae; rami styli 1 mm longi nigro-viridi; achaenia fuscata 3.7–4 mm longa 0.7–1 mm lata incurvata ad basim valde attenuata ad apicem paululum attenuata ad basim valde 5-callosa 10-costata costis latis contiguis convexis glabris; pappus albus 3 mm longus tenuissimus mollis caducus.

Annual, 5–6 dm high; stems erect, rather stout, green, striate, hispidulous, 3-furcate; cauline leaves amplexicaul, auriculate, the lower ones pinnately parted, uppermost entire; branches elongated, cymosely branched above, bearing subcorymbiform clusters of 2–4 heads, the branchlets and peduncles densely gland-pubescent; heads small, about 20-flowered; involucre dark green, campanulate, 7–8 mm high, 4–5 mm wide at middle; outer bracts 6–8, very small, lance-linear, acuminate; inner bracts 12–15, lanceolate, acute, innermost broadly membranous-margined, densely gland-pubescent or -setulose, appressed-pubescent with very short white hairs on inner face, becoming incurved, strongly carinate and pale spongy-thickened in fruit, ultimately reflexed; receptacle areolate, glabrous; corolla 6–7 mm long; ligule 1.5 mm wide, pubescent toward base; corolla tube 2–2.25 mm long, densely pubescent with several-celled tortuous hairs; anther tube about 3×1 mm dis., yellowish-green; appendages about 0.5 mm long, narrow, acute; filaments about 0.5 mm longer; style branches 1 mm long, 0.1 mm wide, dark green; achenes light brown, 3.7–4 mm long, 0.7–1 mm wide, \pm curved, more strongly attenuate toward the base than the apex, constricted below the narrower pappus disk, with a strong 5-lobed basal callosity, 10-ribbed, ribs close, strong, broadly rounded, glabrous; pappus white, 3 mm long, very fine, soft, caducous. Flowering June–July; flowers yellow.

Known only from the type locality in N.W. Syria.

Monomorphic.

Syria: Amanus, Mt. Dümanly, 700–1200 m, *Haradjian 3719* (DL, fragments in UC).

Relationship

C. amanica is beyond question a distinct species. Although its achenes show general resemblance in shape to those of *Arnoseris minima*, they are actually more like those of *C. Stojanovi*, and the broadly rounded ribs resemble those of *C. bupleuri-folia*. The dense glandular pubescence on branches and peduncles resembles that of *C. pterothecoides*; and *C. amanica* is intermediate between that species and *C. Stojanovi* in size of flower heads, outer involucre bracts, anther tubes, and style branches; although the corolla is somewhat shorter than in *C. Stojanovi*. Unfortunately the type itself is an incomplete specimen, the caudical leaves being entirely lacking. But, from the similarities mentioned above, there is no reason to question its classification in this section. Furthermore, its geographical location is in the area occupied by this group.

140. *Crepis Stojanovi* Georg.

Mitt. Bulgar. Bot. Gesellsch. (Bull. Soc. Bot. Bulgarie) 1: 67. 1927. (Fig. 209.)

Annual, 3.5–4 dm high; caudical leaves numerous, ascending, up to 15 cm long and 3 cm wide, obovate, acute, coarsely pinnately dentate, gradually attenuate into a winged petiole, pubescent on both sides and on the margin with short fine white glandular or glandless hairs, and \pm pubescent along midrib with long white erect glandless hairs; cauline leaves reduced, bractlike, or in cultivated specimens up to 6 cm long, similar to caudical leaves or linear, entire; stems 1–3, or more in cultivated specimens, erect or ascending, terete, fistulose, striate, pubescent below with long white glandless hairs, corymbosely branched above with few or many heads; peduncles 1–5 (10) cm long, slender, glabrous or sparsely canescent-tomen-

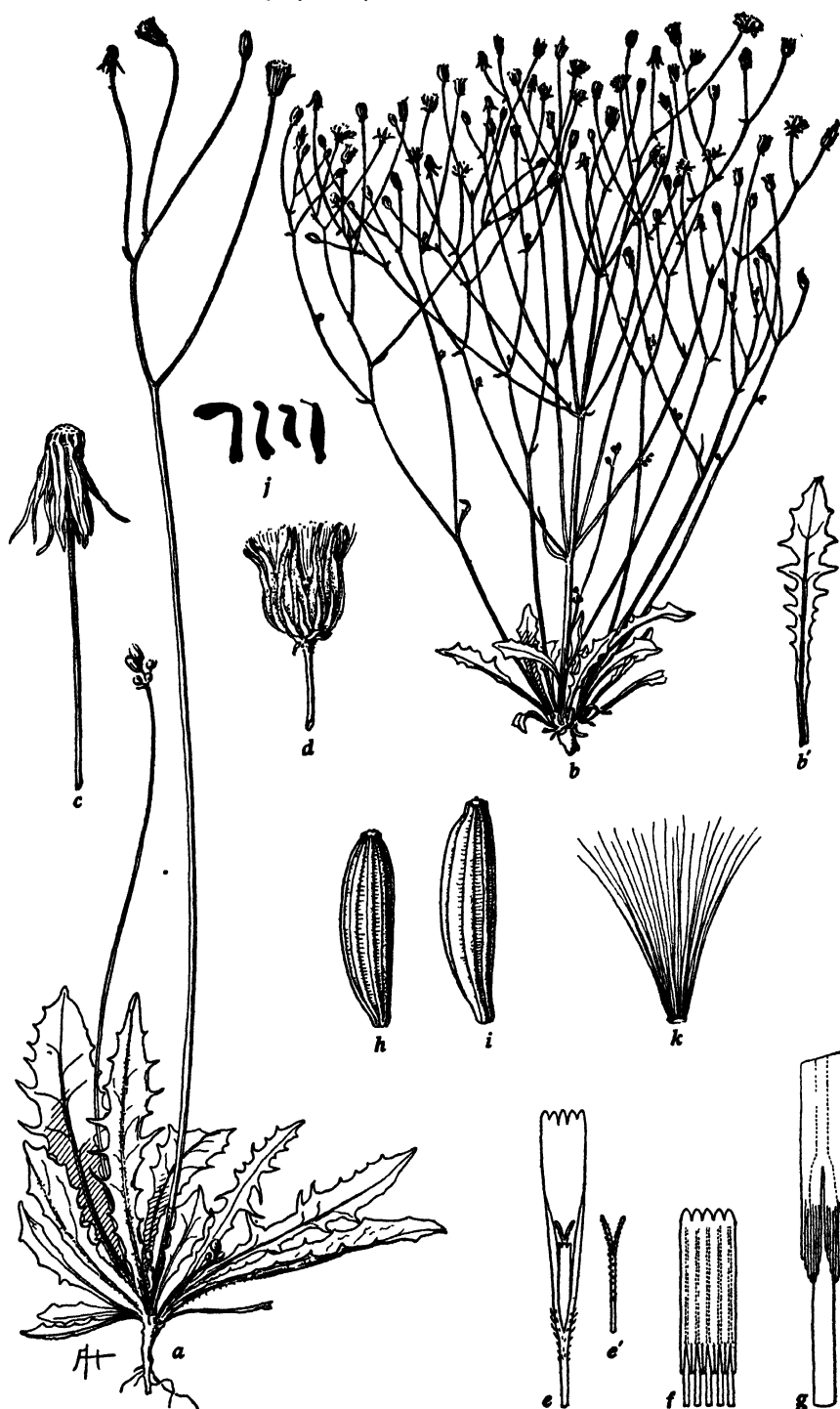


Fig. 209. *Crepis Stojanovi*, a, from Stojanoff, Stefanoff, et Georgieff in 1926 (UC 346433); b-k, from hort. genet. Calif. 32.3176-5 (UC 489425): a, plant, $\times \frac{1}{2}$; b, plant, $\times \frac{1}{4}$; b', caudical leaf, $\times \frac{1}{4}$; c, d, heads, $\times 2$; e, floret lacking ovary, $\times 4$; e', style, $\times 4$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, i, achenes, $\times 8$; j, somatic chromosomes, $n=4$, 1250; k, pappus from 1 achene, $\times 8$.

tulose, naked or 1-bracteate; heads erect, small, about 30-flowered; involucre 8 mm high, cylindric before anthesis, becoming urceolate in fruit, ultimately reflexed, glabrous; outer bracts 8–10, very short, ovate or lanceolate, acute or acuminate, like inner bracts, scarious-margined and ciliate at tip, inner bracts 10–14, lanceolate, acute or obtuse at tip, dorsally keeled, keel yellowish, becoming thickened and indurate below, glabrous on inner face; receptacle areolate, naked; corolla about 10 mm long; ligule 1.5 mm wide, teeth 0.3–0.5 mm long, triangular, acute; corolla tube 2.5 mm long, densely pubescent with several-celled acicular hairs up to 0.6 mm long; anther tube 2.8×1 mm dis.; appendages 0.5 mm long, acute; filaments 0.5 mm longer; style branches 1.4 mm long, 0.1 mm wide, yellow with dark green barbs; achenes brown, 3–3.5 mm long, 0.75–1 mm wide, curved, fusiform, usually somewhat broader above the middle, abruptly attenuate to the narrow pappus disk, more gradually attenuate downward and slightly constricted at the narrow calloused base, 10-ribbed, ribs rather prominent, rounded, smooth; pappus white, 3–4 mm long, very fine, soft, united at base and coming away whole, caducous. Flowering May; flowers yellow. Chromosomes, $2n = 8$.

S.E. Bulgaria; endemic and known from only 4 stations northwest and north of Adrianople, near the Thracian border. Found in the lowest and warmest zone in stony places among shrubs on hillsides.

Monomorphic.

Bulgaria: Harmanli, *Stojanoff* in 1911 (Sofia) type; near Kavakli, *Stojanoff et Stefanoff* in 1926 (Sofia); Sakar, plain between Kavakli and the monastery, Sveta Troitza, *Stojanoff, Stefanoff, et Georgieff* in 1926 (UC); Jamboli dist., Bakardjik hills, *Stojanoff* in 1931 (Sofia).

Relationship

Crepis Stojanovi is very distinct from all the other species of this section except *C. amanica* in its brown strongly ribbed achenes which, although different in shape, being wider in the upper half, constricted at the summit, and gradually attenuate toward the base, somewhat resemble those of *C. nicaeënsis*. Its chromosomes, however, are closely similar to those of the other species in this section, which have been examined cytologically, and differ from those of *C. pulchra* only in minor details, particularly in absence of the distal satellite on the C chromosome. At the same time, it differs from *C. pulchra* in numerous morphological features and is relatively precocious. Furthermore, hybrids between the two species have proved to be completely sterile. Hence it appears that the two species differ greatly in their genetic constitution. On the basis of size of flower heads, flower parts, and achenes, this is the most reduced species in the section.

141. *Crepis pterothecoides* Boiss.

Fl. Orient. 3: 850. 1875. (Fig. 210.)

Annual, 1–3 dm high; root slender, elongated, slightly thickened near the short scarcely exanded caudex; caudical leaves rosulate, about 3 cm long, 1 cm wide (in cult. spec. up to 15 cm long, 3 cm wide), oblanceolate, acute, dentate to pinnately lobed with acute triangular or oblong segments, attenuate into a short winged petiole; cauline leaves mostly reduced, bractlike, the lowest 2 cm long, 0.5 cm wide (in cult. spec. up to 10 cm long, 3 cm wide), lanceolate, acute or acuminate, shortly petiolate or sessile; stem divaricately few-branched near the base, branches elongated, arcuately ascending, remotely cymosely branched, few headed, or stem occasionally simple, erect, forked near summit, 2-headed, or sometimes the stem and bases of branches very short, the slender arcuate peduncles forming a low cluster; peduncles 1.5–6 cm long (or longer in cult. spec.), strict or arcuate, slender, finely



Fig. 210. *Crepis pterothecoides*, a-f, from isotypes, *Kotchy 33* (B, MW); g-m, from *Eig* in 1932 (UC 489385); n-q, from *Eig* in 1932 (UC 489383); r-x, from hort. genet. Calif. 33.3232 (UC 506836): a, plant, $\times \frac{1}{2}$; b, fruiting head, $\times 2$; c, inner involucre bract, $\times 4$; d-f, 2 achenes and a pappus seta, $\times 8$; g, plant, $\times \frac{1}{2}$; h-j, 2 achenes and a pappus seta, $\times 8$; k, floret lacking ovary, $\times 4$; k', detail of ligule teeth, $\times 50$; l, anther tube, $\times 8$; m, detail of appendages, $\times 32$; n, plant, $\times \frac{1}{2}$; o-q, 2 achenes and a pappus seta, $\times 8$; r, floret lacking ovary, $\times 4$; s, anther tube, $\times 8$; t, detail of appendages, $\times 32$; u-w, 3 leaves from a cultivated plant derived from the plant shown in n, $\times \frac{1}{2}$; x, somatic chromosomes, $n = 4$, $\times 1250$.

gland-pubescent; heads about 25-flowered; involucre cylindric-campanulate, 10–14 mm long, 4–6 mm wide at middle in fruit, densely and finely gland-pubescent and sometimes finely setulose near base; outer bracts 10–14, unequal, longest $\frac{1}{3}$ to $\frac{1}{2}$ as long as the inner, lanceolate, acute or acuminate; inner bracts 12–16, lance-linear, acute or acuminate, membranous-margined, white-ciliate at tip, very finely and sometimes sparsely pubescent on inner face, becoming strongly carinate, pale spongy-thickened dorsally, incurved and ultimately reflexed; receptacle areolate, glabrous; corolla 10–13 mm long; ligule 2.25–3 mm wide; teeth 0.2–0.7 mm long; corolla tube 3–3.5 mm long, pubescent with several-celled acicular hairs 0.1–1 mm long; anther tube (3) 3.75×1.2 mm dis.; appendages 0.4–0.7 mm long, oblong, acute; filaments 0.4–0.5 mm longer; style branches 1.3–1.5 mm long, 0.1–0.15 mm wide, yellow; achenes uniform, 6.5–8.5 mm long, 0.3–0.5 mm wide, gradually attenuate upward, usually into a definite beak 2–3 mm long, with expanded pappus disk, constricted above the pale-calloused hollow base, weakly striate, finely spiculate toward apex; pappus white, 3–5 mm long, 2-seriate, very fine, soft, caducous. Flowering May–July; flowers yellow, ligules reddish-purple on outer face. Chromosomes, $2n=8$.

Heteroderis pterothecoides O. Kuntze, Gen. 1: 346. 1891.

Local in E. Anti-Liban (Lebanon) and in Jebel Druz, gravelly and stony places, sometimes among shrubs or trees, on slopes and along wadies, 1500–1700 m. Acc. to Post (155), the species is endemic in Anti-Liban; but in herb. Cosson there is a specimen (*Kotschy* 268) collected in a field of grain near Eden (= Ehden, Liban ?) which, in the absence of achenes, could not be definitely identified. Also in the same herbarium is a specimen (*de Heldreich* in 1868) collected near Alouistena in Arcadia at 909 m elevation which is apparently this species. Since *de Heldreich* collected in Asia Minor as well as in Greece, it is possible that this plant came from Syria and was incorrectly labeled with respect to locality. No other collection of *C. pterothecoides* from Greece is known to me, and the probability is remote that this species actually occurs in Greece because the very precocious nature of *C. pterothecoides* indicates that it is adapted to more arid conditions than those of Arcadia. Finally, the last specimen cited below is not from Anti-Liban, but from an isolated upland 75–100 km southeast of Damascus; the station, El-Kefr, is not known to me.

Monomorphic, so far as known.

Syria: Anti-Liban, around Zebdaine, near Damascus, summit of Mt. Garbus, 1515 m, *Kotschy* 33 (B, PC, MW, UC) isotypes; Anti-Liban, ascent to E. slopes, Wadi Zemerani, near village Jerijir, fields and field borders, 1600 m, *Eig and Zohary* in 1932 (UC, HU); Anti-Liban, E. slopes, Wadi Zemerani, among *Crataegus* bushes, 1730 m, *Eig and Zohary* in 1932 (UC, HU); ex hort. genet. Calif. 34.3232–6, cult. from seeds obtained from the preceding collection (UC); Djebel Drouz (= Jebel Druz), environs of El-Kefr, among *Quercus coccifera*, *Eig and Zohary* in 1932 (UC, HU).

Relationship

Crepis pterothecoides, as its name suggests, shows general resemblance to *C. sancta bifida* or *C. sancta obovata*, but the resemblance is only superficial. In all critical details, including chromosome morphology, it is closest to *C. pulchra*, although it is very distinct from that species in its uniform definitely beaked achenes. It also differs from *C. pulchra* in other important details, such as pubescence on inner face of the inner involucreal bracts, the relatively broad ligules and anther appendages, the yellow style branches, and the straight, 2-seriate pappus bristles. In the small size of the very precocious plants and the beaked achenes it is a more advanced species than *C. pulchra*. Hybrids between the two species were found to be highly fertile, but apparently they are completely isolated in nature. Since a few

collections of *C. pulchra* have been made in central Syria, it is possible that plants of the two species might rarely occur contiguously; but even so, natural crossing would be very unlikely to occur because of the difference in time of flowering, *C. pterothecoides* being very precocious, whereas *C. pulchra* is characterized by a relatively long period of vegetative growth.

For a discussion of the types of isolation involved in the evolution of this group of closely related species, see Part I, page 150.

SECTION 20. HOSTIA

All the species in sec. *Hostia* are characterized by an annual or monocarpic life cycle. The plant is pubescent or hispid; the heads mostly large or medium and many-flowered, the inner involucre bracts becoming strongly carinate, enclosing the marginal achenes, and spongy-thickened or indurate; the achenes either uniform or biform but the inner at least always long-beaked and with 10–20 fine ribs or striae. Morphological, genetical, and cytological evidence all points to the close interrelationships of the species in this section. (*C. tybakiensis* is known only from the

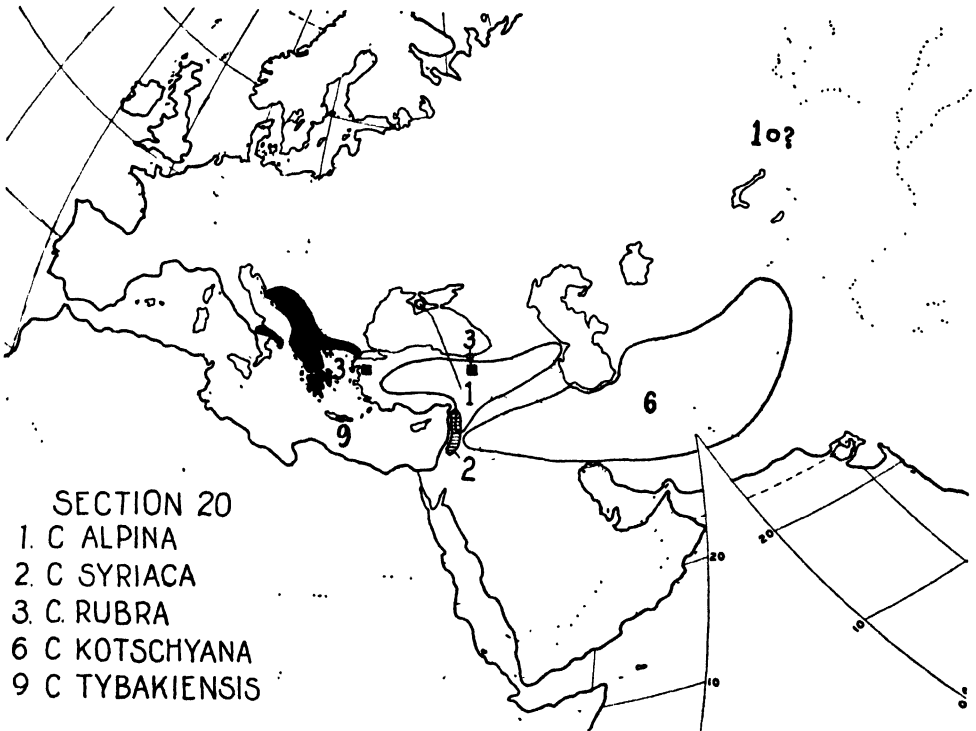


Fig. 211. Geographic distribution of 5 of the 9 species in sec. 20. In addition to the continuous distribution of *C. alpina* from W. Asia Minor to the Caucasus (1), it also occurs in Crimea and it has been reported, without verification, from the Altai. Two isolated stations in Asia Minor for *C. rubra* are shown by solid squares. This species occurs in S.W. Italy as well as in the Balkan Pen. Based on Goode *Base Map No. 201 PC*. By permission of the University of Chicago Press.

type collection, and *C. Schimper* has not been cultivated; but the morphological resemblance of both species to the other species in the section is very strong.) The most convincing evidence on interrelations in this section has been obtained recently by Mrs. Walters (M. Sherman), who studied the meiotic chromosomes of hybrids between *C. Kotschyana*, the only 4-paired species in the section, and *C. alpina*, *C. syriaca*, *C. rubra*, *C. foetida*, *C. eritreensis*, and *C. Thomsonii*, all with 5 pairs of chromosomes. From the pairing behavior of the chromosomes in the F_1 hybrids it is clear that each of the 5-paired species has certain chromosome segments that are homologous with certain segments in the chromosomes of *C. Kotschyana*. This indicates a common ancestry for all the species in the section. The geographic distribution of the 9 species (see figs. 211 and 212) is obviously consistent with the foregoing conclusion. On the basis of certain morphological and cytological pecu-

liarities, however, 4 subgroups exist: (1) *C. alpina* and *C. syriaca*; (2) *C. rubra* and *C. tybakiensis*; (3) *C. foetida*, *C. Schimperii*, *C. eritreënsis*, and *C. Thomsonii*; (4) *C. Kotschyana*.

(1) *C. alpina* and *C. syriaca* are very close species, and hybrids between them were moderately fertile. Yet they differ in numerous characters as well as in the peculiar supernumerary chromosomes which are often present in *C. syriaca* (q.v.). Although the distributional areas of the two species overlap in N. Syria, yet no intergrading variants between them have been reported in the wild. Apparently the two species are somewhat isolated altitudinally, since *C. alpina* is known to occur at stations

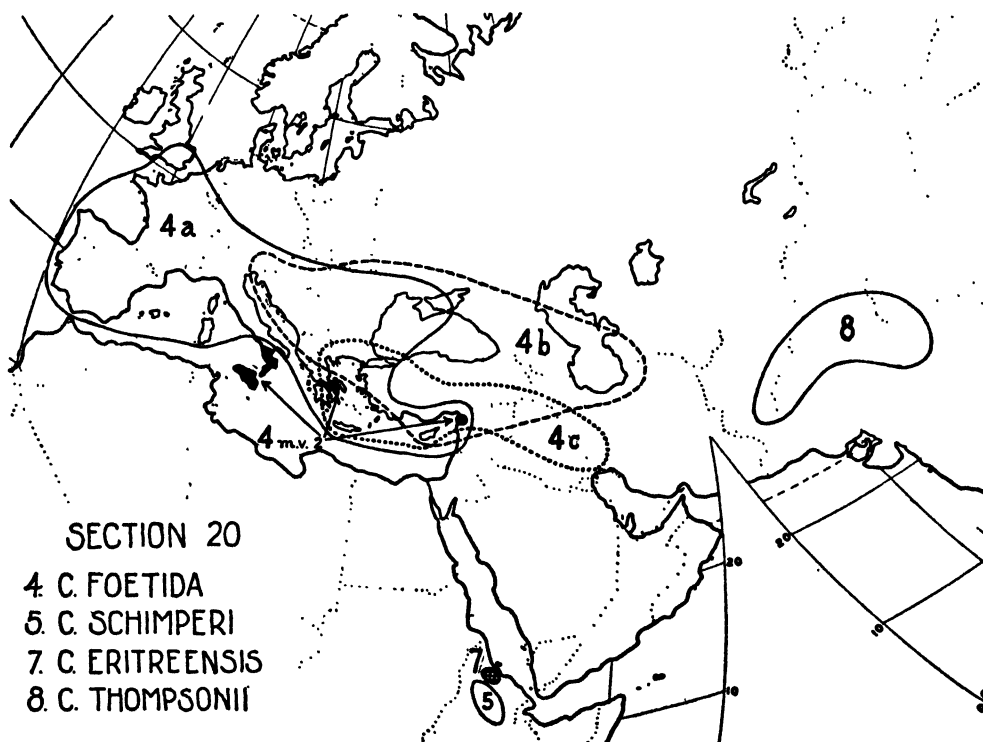


Fig. 212. Geographic distribution of 4 of the 9 species in sec. 20. Each of these distributions is continuous, except that of *C. foetida vulgaris* m.v. 2 which occurs in Sicily, Calabria, E. Greece, and N.W. Syria. Based on Goode Base Map No. 201 PC. By permission of the University of Chicago Press.

from near sea level up to 1200 m altitude, whereas *C. syriaca* occurs at elevations from 600 to 1700 m, the highest being under subalpine conditions. Therefore, the treatment of these two entities as distinct species seems to be warranted.

(2) *C. rubra* and *C. tybakiensis* are very similar, and differ from all other species in the section in their scapose habit. They are similar in leaf shape and in the pale glabrous outer involucre bracts which somewhat resemble those of the two preceding species. Their achenes are also similar, although much reduced in *C. tybakiensis* (q.v.).

(3) That *C. foetida*, *C. eritreënsis*, and *C. Thomsonii* comprise an *Artenkreis*, cenospecies, or superspecies was shown by Babcock and Cave (124–160) on the basis of genetic research. Although hybrids between the three species are more or less fertile and Mendelian inheritance occurs in numerous characters, yet their complete geographic isolation (see fig. 212), together with the morphological and physiologi-

cal differences between them, is considered sufficient reason for their maintenance as species. This conclusion is supported by the cytogenetic evidence of Sherman from hybrids between each of these species and *C. Kotschyana* (see below). The probable phylogenetic relations between the three species are indicated in fig. 222 (p. 706), in which the large circle represents *C. foetida* sen. lat., and the smaller shaded circles at the left, *C. eritreënsis* and *C. Thomsonii* (cf. B. and Cave, *op. cit.*). Since *C. Schimperii* of central and N. Abyssinia has not been observed in living condition, it can only be stated that morphologically it certainly belongs in this subgroup. Apparently it is isolated from *C. eritreënsis* both geographically and altitudinally.

(4) *C. Kotschyana*, the only species in the section with 8 chromosomes in its somatic cells, is unusually interesting because of its genetic relations with six other species in this section and because it is one of the more advanced species in the section. Its phylogenetic position, as based on morphology, is in line with the cytogenetic evidence of Sherman that it was certainly derived from a 10-chromosome ancestor and that it had a common ancestry with its 5-paired relatives. Its wide distribution (fig. 211), overlapping those of *C. Thomsonii* on the east and *C. foetida* on the west, is also of interest because it shows that *C. Kotschyana* is a successful species in a region of high aridity. Furthermore, on account of the difference in chromosome number it certainly acts as a biotic barrier between *C. Thomsonii* and its close relative, *C. foetida*.

Key to the Species of Section 20

Outer involuclral bracts ovate or broadly lanceolate, imbricate, pergameneous.

Flowers yellow; achenes bifiform, the marginal pale, densely pubescent, with a crown of short hairs surrounding the pappus setae.

Middle cauline leaves entire or denticulate at the rounded base; heads always erect; style branches green; marginal achenes 15–17 mm long; inner achenes 15–20 mm long; pappus 6–7 mm long.....142. *C. alpina*, p. 678

Middle cauline leaves deeply laciniate near the base or acutely auriculate; heads nodding before anthesis; style branches yellow; marginal achenes 5–14 mm long; inner achenes 12–15 mm long; pappus 4.5–5.5 long.....143. *C. syriaca*, p. 681

Flowers pink or white; achenes uniform, the marginal dark brown like the inner, but more coarsely beaked.....144. *C. rubra*, p. 683

Outer involuclral bracts narrowly lanceolate or linear, not imbricate, not pergameneous.

Plant several-stemmed, the stems scapiform, leafless, 1-headed...150. *C. tybakiensis*, p. 718

Plant 1-stemmed, the stem more or less leafy, several or many-headed except in rare 1-headed depauperate plants.

Achenes bifiform, the marginal broader than the inner, more or less attenuate or shortly and coarsely beaked, the inner achenes with a long fine beak, or if marginal achenes sometimes with a long beak (*C. foetida commutata*), then the receptacle paleaceous.

Outer involuclral bracts persisting in mature fruiting heads; inner bracts at maturity broadly convex dorsally, without a definite keel; inner achenes brown; receptacle alveolate, ciliate.

Corolla 9–19 (mostly 11–18) mm long; anther tube 3–4 mm long; style branches 1.5–3 mm long; beak of inner achenes brown. Europe, Asia Minor, Transcaucasia, W. Persia.....145. *C. foetida*, p. 687

Corolla 7–9.5 mm long; anther tube 2 mm long; style branches 0.75–1.25 mm long; beak of inner achenes yellowish. N. India, Afghanistan, Baluchistan.....149. *C. Thomsonii*, p. 713

Outer involuclral bracts disappearing in mature fruiting heads; inner bracts at maturity narrowly convex dorsally, with a prominent narrow yellow keel; inner achenes stramineous; receptacle areolate, with naked fleshy ridges.....147. *C. Kotschyana*, p. 707

Achenes uniform, the marginal shorter than the inner but finely beaked; receptacle not paleaceous.

Plant hispid, especially the involucre, with setiform glandless hairs; branches 2-headed; peduncles longer; style branches 1 mm long; achenes reddish-brown fading to yellowish-brown above, 0.75 mm wide, the ribs stronger, the beak coarser and equal to the body.....146. *C. Schimper*, p. 705

Plant hispidulous with fine soft glandular and glandless hairs; branches mostly 3-headed; peduncles shorter; style branches 1.75–2 mm long; achenes dark brown when mature, 0.5 mm wide, the ribs finer, the beak finer and 2–3 times as long as the body.....148. *C. eritreensis*, p. 711

142. *Crepis alpina* L.

Sp. Pl. 806. 1753. (Pl. 16. Fig. 213.)

Annual, 1–12 dm high; caudical leaves up to 15 cm long, 4 cm wide, obovate-oblong, narrowed toward base, obtuse, denticulate, corneous-mucronate, sometimes with 3–4 irregular usually shallow lobes near apex, puberulent or rarely gland-pubescent; lower cauline leaves similar; middle and upper cauline leaves oblong, ovate or lanceolate, acute or acuminate, amplexicaul, subauriculate, rounded, entire or denticulate at base, uppermost bractlike; stem erect, robust, sulcate, scabridulous, \pm tomentulose, rarely gland-pubescent, cymosely branched from below or above the middle (in reduced forms sometimes 1-headed), branches long, stiffly erect, pendunculate or sometimes 2–3-headed; peduncles gradually thickened near head, striate, scabrous, \pm tomentose; heads erect, large, many-flowered; involucre cylindric-turbinate, 15–22 mm high, 7–15 mm wide at middle, the bracts of two distinct sorts; outer bracts 13–16, in several series, imbricate, $\frac{1}{3}$ as long as inner bracts at maturity, ovate, acute, becoming \pm recurved, scarious, glabrous or tomentulose; inner bracts 10–13, nearly equal, lanceolate, obtuse, scarious-margined, ventrally strigose, dorsally tomentose and densely pubescent with short glandular hairs and longer yellow glandular or glandless bristles, becoming indurate and strongly carinate below, enclosing the marginal achenes, remaining erect at maturity; receptacle concave, areolate-fimbriate, the fimbriae very delicate, white, finely ciliate; corolla 13–18 mm long; ligule up to 1.5 mm wide; teeth 0.8 mm long; corolla tube 4–6 mm long, sparsely beset with stout salient acicular hairs; anther tube yellow, about 4×1.2 mm dis.; appendages 0.4–0.6 mm long, acute; filaments 1 mm longer; style branches green or greenish, 2.5–3 mm long; achenes biform, the marginal 15–17 mm long, curved, gradually attenuate into a coarse beak, strongly narrowed near base, the lower $\frac{1}{3}$ ventrally compressed with a median ridge, ventrally pale, spongy-thickened, densely covered with coarse white trichomes 0.2–0.4 mm long, dorsally light brown, striate, spiculate, with a basal scar 2 mm long; inner achenes 15–20 mm long, light brown, narrowly fusiform, gradually attenuate into a slender paler beak, finely 15-ribbed, spiculate; pappus yellowish white, 6–7 mm long, 3-seriate, coarse to fine, persistent, and on the marginal achenes surrounded at base by a crown of many fine white hairs 0.5–0.7 mm long. Flowering May–July; flowers pale or deep yellow, purplish on outer face of ligules. Chromosomes, $2n = 10$.

Crepis vesicaria Lam., Dict. 2: 178. 1790 non L.

Barkhausia scariosa Moench, Meth. 537. 1794.

Barkhausia alpina Moench, ex Moessler, Handb. ed. 3, 2: 1473. 1833.

Barkhausia alpina DC., Prod. 7: 153. 1838.

Billotia alpina Sch. Bip., ex Winck., Jahrb. Prakt. Pharmac. 4 (nota): 155. 1843.

Barkhausia elata Koch, Linnaea 23: 684. 1850 = m.v. 3.

Anthochytrum alpinum Rehb. f., Ic. Fl. Ger. Helv. 19: t. 81, 1858–1859.

Hieraciodes alpinum O. Kuntze, Gen. 1: 345. 1891.

Europe, in S. Russia and Transcaucasia; Asia, from N. Syria through Asia Minor and eastward to N.W. Persia; in W. Siberia? (Cf. *Gmelin*, cited in de Candolle, 153; and *Pallas*, *Reise* 2: 523. 1773, cited in *Ledebour*, A, 126, R, 818; and in *Krilov*, Fl.

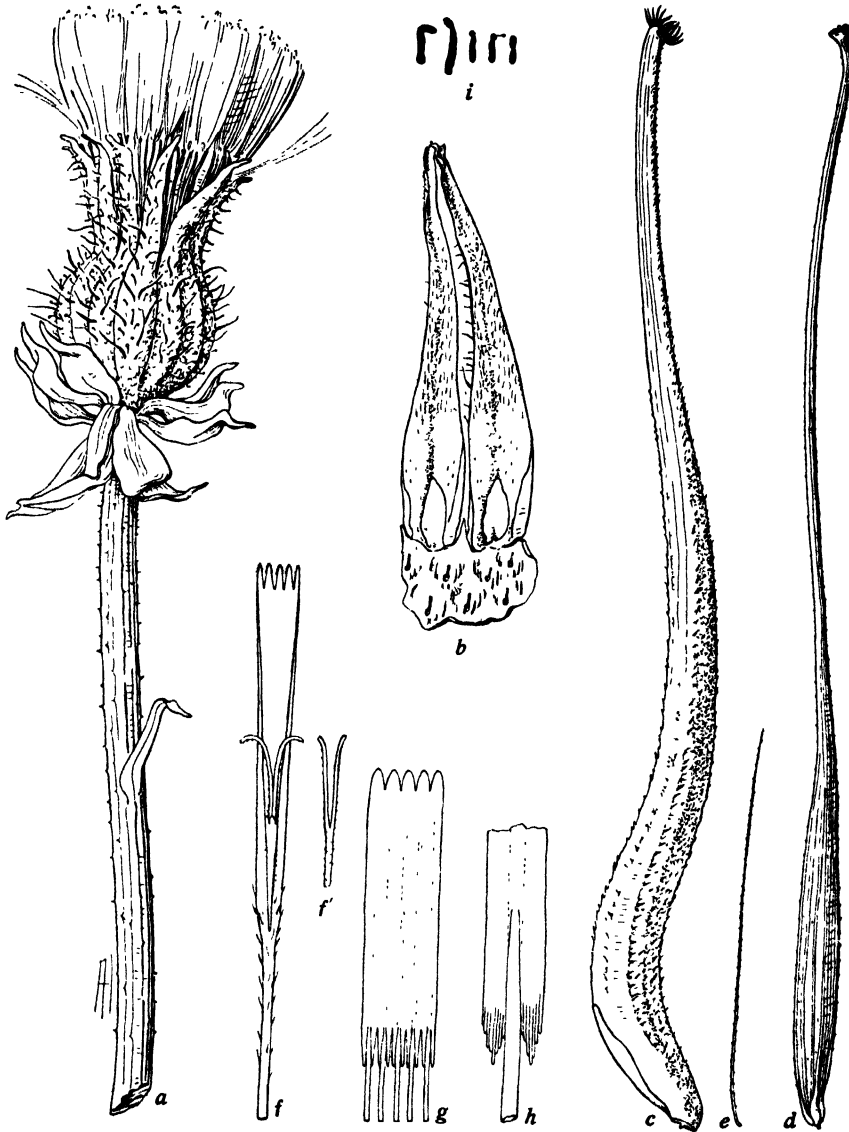


Fig. 213. *Crepis alpina*, from specimen "ex seminibus H.R.P." in 1841 (DS 130741, 130742); *i*, from hort. genet. Calif. 1499 (grown from seeds received from Copenhagen Bot. Gard.): *a*, mature head, $\times 2$; *b*, inner involucral bracts and part of receptacle, $\times 4$; *c-e*, marginal and inner achenes and a pappus seta, $\times 8$; *f*, floret lacking ovary, $\times 4$; *f'*, part of style and branches, $\times 4$; *g*, anther tube, $\times 8$; *h*, detail of appendages, $\times 32$; *i*, somatic chromosomes, $n = 5$, $\times 1250$.

Altaica 3: 754. 1904. It is to be noted that *Ledebour* states that this species is unknown to him in the Altai; also, that *Krilov* cites only *Pallas* as authority for the Altai and, although he mentions also S.W. Tomsk, he cites no specimens. Thus, the occurrence of *C. alpina* in W. Siberia remains in doubt.) Regarding the statements in various floras, for example *de Candolle* (153) and *Fiori* (431), that this

species occurs in N. Italy, since Fiori states that he had seen no specimens from Italy and the only specimens from Europe seen by the present author are from S. Russia, it seems very unlikely that *C. alpina* is indigenous in Italy. Schultz Bipontinus (Jahrb. Prak. Phar. 4: 155. 1841) states that this species was frequently grown in gardens. Therefore, although the type locality given by Linnaeus is "Alpibus Italiae," it seems probable that his specimen came from an Italian botanic garden.

The name is unfortunate because this is a plant of lower altitudes, occurring in plains and valleys from 50 to 1200 m alt. The type and some variants are shown in pl. 16.

Twenty-one accessions of *C. alpina* have been tested in our garden. Although they were highly uniform in the characteristic features of the species, there was evidence of genetic differences in degree of leaf dissection, in presence or absence of glands on leaves and stems, in habit of the plant, in time of maturity, and in color of the ligules. Concerning the latter, it was noted that several accessions from the Caucasus region had deep yellow ligules, whereas the strains from Asia Minor had pale ligules. The Caucasian strains also had glandular pubescence which was lacking in the others. But, until more is known about the variation in these and other characters in both regions, the recognition of different taxonomic entities seems hardly warranted. In this species the individual plant is self-fertile.

Russia: Crimea, Baidar, Laspi Valley, *Callier* in 1895 (B); Crimea, Laspi Valley, *Halacsy* 663 (B, Bur) m.v. 1 and 2; Transcaucasia, Karabagh Prov., *Fischer* in 1832 (DC); Schirwan (Shirvan) *Koch* (B); Schirwan, *Koch* in 1844 (B) m.v. 3. **Asia Minor:** Phrygia, Eskisehir, and Usak, *Krause* 3501, 3399 (UC); Phrygia, Egirdir, *Heldreich* (B); Galatia, near Ankara, *Krause* 4403 (UC) m.v. 1; Galatia, Angora, *Bornmüller* 206B (B) m.v. 1 and 2; Pontus, Amasia, *Bornmüller* 1874 (B) m.v. 2; Pontus, Caraja (= Karakaja ♀) Springs, *Warburg and Endlich* 1109 (B); Kurdistan, Mardin, Senar, *Sintenis* 910 (B). **Syria:** *Labillardiere* (DL); below Djebel Seman, *Haradjian* 2109 (Bur); Aleppo, *Kotschy* (B).

Minor Variants of *C. alpina*

1. (*C. alpina* L. fa. *typica* Bornm., in herb.) Closely similar to Linne's type but has cauline leaves much narrower. *Bornmüller* 206B (B), Angora, Galatia, Asia Minor; *Halacsy* 663 (B, Bur), Laspi Valley, Crimea, Russia.

2. (*C. alpina* L. fa. *simplex* Bornm., in herb.) Similar to m.v. 1 but has simple 1-headed stems. *Bornmüller* 206B (B), Angora, Galatia, Asia Minor; *Halacsy* 663 (B, Bur), Laspi Valley, Crimea; *Bornmüller* 1874 (B), Amasia, Pontus, Asia Minor.

3. (*Barkhausia elata* Koch, *Linnaea* 23[7]: 684. 1850.) A robust form with the outer involucre bracts and cauline leaves lanceolate. Neither young heads nor florets available. *Koch* in 1844 (B). Type locality, plains in alluvial and diluvial soils, up to 30 m alt., Shirvan, Persia.

Relationship

Although this species is sufficiently distinct to have been treated as a monotypic genus by Reichenbach filius and Schultz Bipontinus, yet it is closely related to *C. syriaca*, *C. rubra*, and *C. foetida*. Of these three species, *C. syriaca* is morphologically most similar to *C. alpina*, but it is evidently a different species. As for *C. rubra* and *C. foetida*, the inner achenes of both are similar to those of *C. alpina*; in *C. foetida*, the outer achenes are modified similarly to those of *C. alpina*; whereas in *C. rubra* the scarious outer involucre bracts resemble those of *C. alpina*. Hybridization is possible between *C. alpina* and the other three species and there is much similarity between the karyotypes of the four species. *C. alpina* has also been crossed with *C. Kotschyana*, the only 4-paired species in this section, and from a study of the hybrids homologous segments in the chromosomes of these two species have been demonstrated (Sherman). The same kind of evidence has been obtained from hybrids between five other species in this section and *C. Kotschyana*. Thus, *C. alpina* is genetically connected with the other species in this section.

143. *Crepis syriaca* (Bornm.) Babe.

Univ. Calif. Publ. Bot. 19: 404. 1941. (Fig. 214.)

Annual, 2–4 (6.5) dm high; caudical leaves rosulate, up to 12 cm long, 2 cm wide or larger, oblanceolate, tapering into a winged petiole with clasping base, acute, denticulate, or \pm dissected, the segments unequal, acute, dentate, corneous-mucronate, like the stem and branches sparsely canescent-tomentulose or glabrate; lower cauline leaves similar, middle and upper cauline leaves lanceolate, acuminate, amplexicaul, deeply lacinate near base or acutely auriculate; stem erect, simple, 1-headed, or few-branched above or branched from base upward; branches long, spreading or arcuate, leafy, 1–3-headed; peduncles 0.3–15 cm long, scabridulous, scarcely thickened near head; heads large, cylindric-turbinate, many-flowered, nodding before anthesis; involucre 15–22 mm high, 7–12 mm wide, the bracts of two distinct sorts; outer bracts 12–22, in several series, imbricate, about $\frac{1}{3}$ as long as inner ones at maturity, ovate or lanceolate, acute, scarious, ventrally glabrous, dorsally canescent-tomentose with a dark median line and with or without a single median row of short or long glandless bristles, becoming \pm reflexed at maturity; inner bracts 10–14, nearly equal, lanceolate, obtuse, scarious-margined, ventrally pubescent toward tip with short white hairs, dorsally canescent-tomentose and densely pubescent with short yellow glandular hairs and long glandless hairs which are yellow or yellow with black base or black toward tip of bracts, becoming indurate and carinate below enclosing marginal achenes, remaining erect at maturity; receptacle concave, areolate-fimbrillate, the fimbrillae membranous and finely ciliate; corolla 12–15 (16) mm long; ligule up to 1.25 mm wide; teeth 0.4 mm long, \pm united, concave, obtuse; corolla tube 3–4 mm long, slender, sparsely beset with salient acicular trichomes; anther tube yellow, about 4.5×1.2 mm dis.; appendages 0.7 mm long, obtuse; style branches yellow, about 3 mm long; achenes biform, or the distinctive marginal achenes replaced by inner or intermediate ones; marginal achenes 5–14 mm long, curved, gradually attenuate to summit, strongly narrowed near the calloused base, subterete or strongly angled, the lower half obcompressed, with prominent median ventral ridge bordered by pale spongy-thickened ridges, dorsally light brown, striate, with a basal scar about 1 mm long, pubescent with white trichomes 0.2 mm long; inner achenes 12–15 mm long, light brown, narrowly fusiform, gradually attenuate into a slender paler beak, narrowed at the calloused base, about 15-ribbed, ribs fine, spiculate; pappus yellowish-white en masse, 4.5–5.5 mm long, 2-seriate, rather fine, persistent, and on marginal achenes surrounded at base by a crown of many fine hairs 0.3–0.4 mm long. Flowering Mar.–June; flowers yellow. Chromosomes, $2n = 10 + 0\text{--}8$ supernumerary chromosomes (Cameron, D. R., Univ. Calif. Publ. Agr. Sci. 6: 257–286, 1934).

Crepis alpina L. var. *syriaca* Bornm., Beih. Bot. Centralb. 31 (2): 237. 1914.

N. Syria to N. Palestine, montane.

Monomorphic.

Syria: Mt. Lebanon, S. side, subalpine cliffs west of village Bhamdun, 1400 m, Bornmüller 12086 (type Bornm, B, MW); Mt. Lebanon, Hasroun, bank of wadi, 1200–1300 m, Zohary in 1931 (UC); Lebanon, between Hasroun and Bakafra, 1300–1700 m, Zohary in 1931 (UC); Djebel Arlain, environs of Eriha, Eig and Zohary 3229 (UC); Ziarath-Dagh, Belled e Scheik, field borders, Eig and Zohary 3231 (UC); between Antiochia and El Urdu, environs of Ouschahadly, a sacred forest of *Quercus infectoria*, Eig and Zohary 3230 (UC) reduced form; base of Akher Dagh, near Masarit, 850 m, Haradjian 1511 (DL); environs of Homs, 600 m, Haradjian 3275 (DL). Locality dubious (N.E. Arabia ?): lower reg. of Djebel Seman (= Senam ?), 636 m, Haradjian 2109 (DL). Palestine: reg. of Jordan R., Ibl es-Soki (= Ibl es Suk ?) ex Herb. Coll.

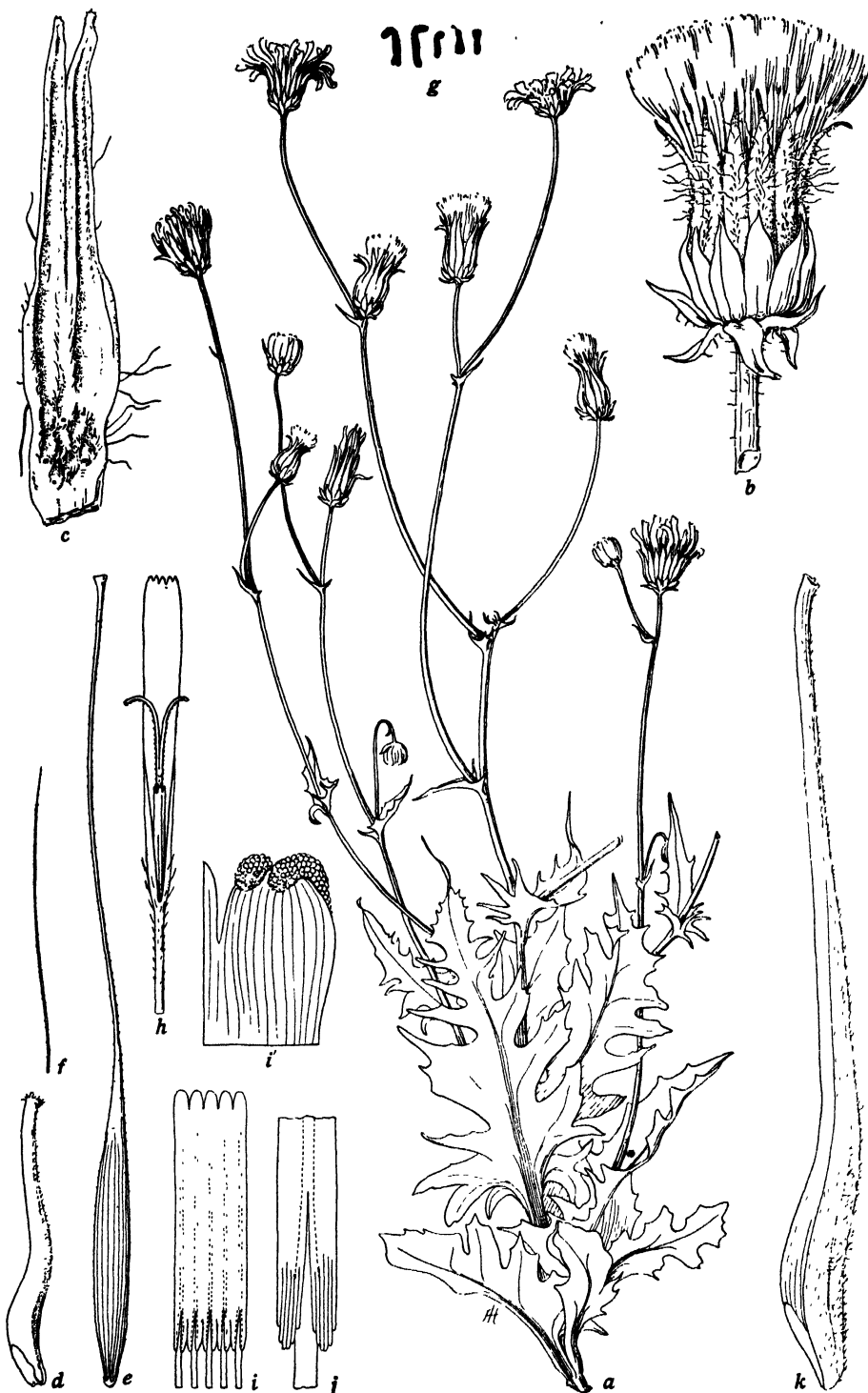


Fig. 214. *Crepis syriaca*, *a*, *h-j*, from type collection, Bornmüller 12086 (B, Bornm); *b-g*, from Chijik in 1924 (UC 313831, 313832); *k*, from Zohary in 1931 (UC 466657): *a*, plant, $\times \frac{1}{2}$; *b*, head, $\times 2$; *c*, ventral surface of 2 bracts and adjacent receptacle, $\times 4$; *d-f*, marginal and inner achenes and a pappus seta, $\times 8$; *g*, the haploid set of a 10-chromosome plant, $\times 1250$; *h*, floret lacking ovary, $\times 4$; *i*, anther tube, $\times 8$; *i'*, detail of 2 united ligule teeth showing glandular hood, $\times 32$; *j*, detail of appendages, $\times 32$; *k*, marginal achene, $\times 8$.

Syr. Protest. 633, 634 (K); Galilee, environs of the Menahamiah Company, *Chijik* in 1924 (UC); Tiberius, *Eig* in 1922 (HU); Plain of Esdraelon, Kefar Jehezekiel, slopes of wadi, *Eig* in 1923 (HU).

The close relationship of *Crepis syriaca* to *C. alpina* is indicated by the fact that Bornmüller first named it as a variety of the latter. Bornmüller noted, however, that *C. syriaca* is very distinct in its divaricate habit and smaller heads and achenes. There is considerable variation in head size in both species, also in length of achenes. Additional distinguishing characters of *C. syriaca* are given in table 16. The variation in number of chromosomes, from 10 to 18 (cf. Cameron, Univ. Calif. Publ. Agr. Sci. 6: 257–286. 1934), adds considerable interest to this little-known species. The situation concerning chromosome numbers found in *C. syriaca* is similar to that reported by Miss Sorokin in *Ranunculus acris* (Amer. Nat. 41: 574. 1927) and by Randolph in maize (Cornell Univ. Agr. Exp. Sta. Mem. 117: 3–144. 1928). The

TABLE 16

SYNOPTICAL COMPARISON OF THE CHARACTERS DISTINGUISHING *CREPIS SYRIACA* FROM *C. ALPINA*

Character	<i>C. syriaca</i>	<i>C. alpina</i>
Habit	low, spreading	tall, erect
Herbage	light green, lacking tomentum	gray, tomentose
Caudical leaves	oblanceolate, acute, dentate or runcinate-pinnatifid or pinnately parted, these segments acute, dentate	obovate-oblong, obtuse, denticulate, sometimes with 3–4 irregular shallow lobes near apex
Cauline leaves .	lacinate at base	entire or denticulate at base
Position of heads	nodding before anthesis	erect before anthesis
Heads	fully expanded in anthesis	partly expanded in anthesis
Ligules	deep yellow	pale yellow
Anther tube	appendages 0.7 mm long, obtuse	appendages 0.4–0.5 mm long, acute
Achenes	about 14 mm long, not always sharply divided into two types	about 18 mm long, of two distinct types, marginal and inner
Pappus	4.5–5.5 mm long	6–7 mm long
Flowering time	about 108 days after planting	about 135 days after planting

nodding buds of *C. syriaca* suggest the possibility that it originated as the result of hybridization between *C. alpina* and *C. rubra*. This possibility, however, may be rejected on the basis of comparative morphology and geographic distribution. A more acceptable hypothesis, proposed by Cameron (*loc. cit.*), assumes the origin of *C. syriaca* through hybridization of typical *C. alpina* and a Caucasian form of *C. alpina*, followed by chromosomal alterations in the hybrid derivatives. The basic karyotype of 5 chromosomes found in this species is shown in fig. 214, *g*. It was reported by Cameron (*loc. cit.*) that the supernumerary chromosomes, which may range in number from 0 to 8, resemble a type with a large satellite that is sometimes found in *C. rubra* (cf. fig. 216, *g*); and a similar satellited chromosome has been observed in one of the Mediterranean variants of *C. foetida vulgaris*. Such observations go along with the morphological evidence indicating a common ancestry for this whole section. Much more convincing evidence in support of the concept of genetic unity in this section has more recently come from the cytogenetic research of Sherman (see Part I, p. 21).

144. *Crepis rubra* L.

Sp. Pl. 806, 1753. (Figs. 215, 216.)

Annual, 0.4–4 (mostly 1–2.5) dm high; root vertical, slender; caudex \pm swollen, with one, few, or many stems; caudical leaves few or many, 2–15 cm long, 0.5–3 cm wide, oblanceolate, acute, denticulate, dentate or runcinate-pinnatifid with triangular or lanceolate acute segments, attenuate into a long or short winged petiole,



Fig. 215. *Crepis rubra*, from *Guiol 208* (UC 429474): a, plant from a moist, shady place, $\times \frac{1}{2}$; b, fruiting head, $\times 2$; c, c', inner involucre bract, outer and inner face, $\times 4$; d, marginal achene enclosed in bract, $\times 8$; e-g, inner achenes and a pappus seta, $\times 8$; h, detail of receptacle, $\times 25$.

pubescent on both sides with pale glandless hairs; cauline leaves few, mostly small and bractlike, the lower ones similar to caudical leaves or sessile; stems scapiform, 1-headed, or 1–2-branched near the base, the branches pedunculate or rarely 1-furcate with long pedunculate branchlets, mostly decumbent or semidecumbent or sometimes strict, terete, puberulent, tomentulose or glabrescent; peduncles conescent-tomentose near the head, bent downward before anthesis, becoming somewhat thickened and sulcate in fruit; heads medium to large, 40–100-flowered; involucre cylindric-campanulate, in fruit 11–15 mm high, 4–7 mm wide at middle; outer bracts 10–12, often with 2–4 closely subtending, unequal, the longest $\frac{1}{2}$ as long

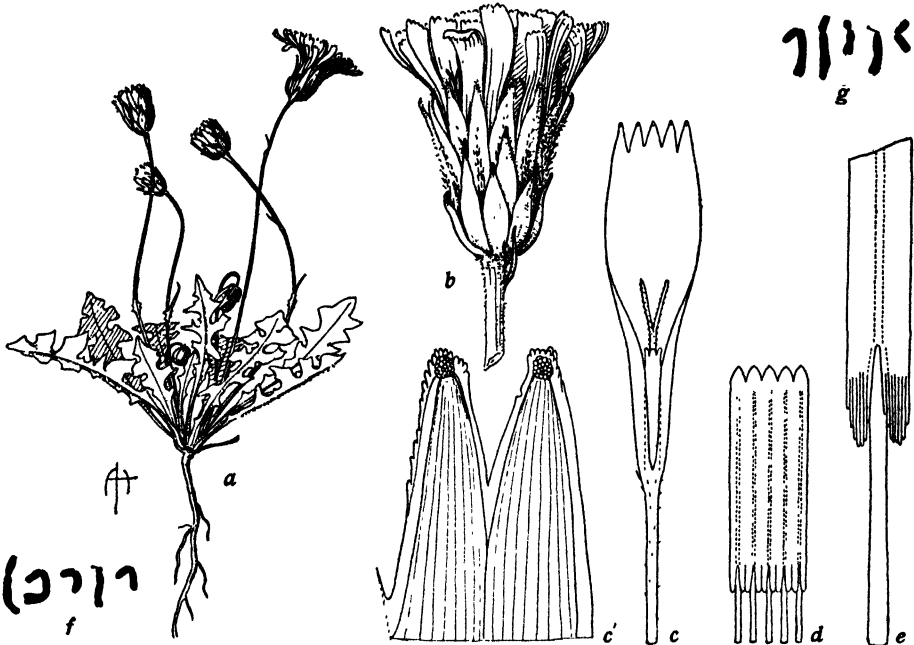


Fig. 216. *Crepis rubra*, a–f, from *Guiol* 208 (UC 429476); g, from hort. genet. Calif. 3452 (grown from seed received from Copenhagen Bot. Gard.): a, plant from a dry, sunny place, $\times \frac{1}{2}$; b, flowering head, $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule teeth, $\times 50$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, somatic chromosomes of a seedling derived from *Guiol*'s wild specimens, $n = 5$, $\times 1250$; g, somatic chromosomes of a cultivated strain, $n = 5$, $\times 1250$.

as inner bracts in anthesis, $\frac{1}{4}$ – $\frac{1}{3}$ as long in fruiting heads, ovate-lanceolate, acuminate, glabrous or puberulent, imbricate and pale yellowish-green in anthesis, becoming scarious and lax; inner bracts 8–14 (mostly 10–12), lanceolate, acute or obtuse, usually darker in median zone and paler toward margin, sometimes with a pale median stripe, sparsely to densely pubescent with short or long pale gland hairs mostly on lower half, canescent-tomentulose toward apex, appressed-pubescent on inner face, becoming strongly carinate, infolding marginal achenes, pale spongy-thickened on lower half; receptacle alveolate, fimbriae densely ciliate; corolla about 17 mm long; ligule 3 mm wide; teeth 0.8–1 (2) mm long; corolla tube 5.5 mm long, sparsely pubescent with fine acicular hairs up to 0.1 mm long; anther tube 3.7×1.2 mm dis.; appendages 0.4 mm long, oblong, acute, united, very thin and delicate; style branches 1.75 mm long, 0.15 mm wide, yellow; achenes dark brown, the marginal shorter, curved, more coarsely beaked, the inner longer, straight, more finely beaked; marginal achenes 8.5–9 mm long, about 0.6 mm wide, uniformly dark brown or paler near apex, subterete, strongly attenuate into a coarse beak, with

slightly expanded pappus disk, constricted at the small calloused base, about 10-ribbed, densely and strongly spiculate; inner achenes 12–21 mm long, 0.4–0.5 mm wide, terete, gradually attenuate into a long rather fine pale beak, with expanded pappus disk, slightly narrowed to the pale-calloused hollow base, 15–20-ribbed, ribs narrow, close, finely spiculate; pappus yellowish-white or dusky, 5–8 mm long, 3-seriate, setae nearly equally fine, the coarsest 28–34 μ wide at base, rather stiff but pliable, persistent. Flowering Apr.–June; flowers pink or white. Chromosomes $2n = 10$.

Picris rubra Lamk., Fl. Fr. 2: 109. 1778.

Barkhausia rubra Moench, Meth. 537. 1794.

Hostia rubra Cass., Dict. Sc. Nat. 21: 443. 1821.

Crepis incarnata Vis., Stirp. Dalm. Sp. 17, t. 6, f. 2. 1826, non Tausch.

Anisoderis rubra Cass., Dict. Sc. Nat. 48: 429. 1827.

B. purpurea Ung., Reise 125. 1862, non (Biv.) Guss.

Hieraciodes rubrum O. Kuntze, Gen. 1: 344. 1891.

S. Italy, Dalmatia, Albania, Macedonia, Thrace, Greece, Crete, and Asia Minor. Long since cultivated in gardens throughout the world and occasionally feral.

Except for the two flower-color types, the most striking variations are in sizes of the plants. Under xerophytic conditions they are more or less depauperate and are sometimes reduced to a short slender scape with a few tiny basal leaves. Under cultivation, strains from various localities exhibit numerous minor differences in leaves, stems, and flowers, including variations in color of the anther tube. The selected strains supplied by seedsmen are usually much more vigorous and bear larger flowers than strains introduced from the wild.

Italy: Apulia, *fide* L., Sp. Pl. loc. cit. (L) type; Apulia, Gussone in 1831 (DC); Apulia, Foggia dist., Lucera, about 250 m, Villani in 1912 (K, Bur); Naples, Reynier in 1814 (K); near Naples, Coqueray in 1844 (US); *ibid.*, Reimbolet in 1871–2 (Mo). **Dalmatia:** Spalato, Pichler in 1870 (Bur, K, Mo, UC); Bua I., Sterneck in 1899 (US); Perkovic, Burnat *et al.* in 1905 (Bur). **Albania:** Kusenta reg., Janius dist., near Mt. Cinka, Baldacci in 1896 (K); below Mt. Guka, Baldacci in 1896 (Bur). **Greece:** Corfu, S. Deka, Baenitz in 1896 (US); Corfu, Potamo, Becknell in 1891 (Bur); Zante, Margot in 1837 (DC); without locality, Aucher 3414 (DC); Laconia, Menelaos, in 1862 ex herb. Mill (K); Attica, Mt. Parnes, Climendi, Guiol 208 (UC) sun and shade forms; foot of Mt. Parnes, among stones, 325 m, Demades in 1921 (UC); Thessaly, Mt. Pelion, near Volo, de Heldreich in 1883 (Bur); Mt. Pelion, Trikkeri, Miss Topali in 1937 (UC); Thessaly, Kalampaka, Freyn in 1882 (Bur); *ibid.*, Hagios Stephanos, Sintenis 82 (K); Thessaly, east of Mt. Ossa, between Selitsani and Karitsa, about 800 m, Miss Topali in 1938 (UC); Ionian Is., Corigo I., Druce (Oxford); Crete, Leuka Mts., 1677 m, Battye in 1909 (K); Lasithion Prov., Sitia, Gandoger in 1914 (Mo). **Turkey:** Trojan field (site of Troy ?), Schmidt in 1864 (B); W. Kurdistan, "Omankioi" (= Omar Keui, Omer Koi, Omeranli), east of Marash and south of Kharput, Calvert in 1882 (B).

Relationship

Crepis rubra follows *C. alpina* and *C. syriaca* in degree of primitiveness as compared with the other species in this section. The individual floret is larger in *C. rubra* than in the two species just mentioned, but the involucre, although similar, is smaller and the aggregate inflorescence has been reduced to scapiform habit. Also, the marginal achenes are not as large or as distinctly different from the inner achenes in *C. rubra*, and the anther tube and appendages are smaller. But, in spite of its pink and white flower colors, *C. rubra* may be considered a fairly primitive species. In this connection its geographic distribution is especially interesting. Although only two collections of this species are known to the author from Asia Minor, it does not seem very likely that either was a feral plant. If the species is actually indigenous in Asia Minor, this provides another definite connection of a fairly primitive species with the assumed center of origin of the genus.

145. *Crepis foetida* L.

Sp. Pl. 2: 807. 1753. (Pls. 17, 18. Figs. 217–222.)

Annual, rarely biennial, or short-lived perennial (?), 1–5 dm high, \pm hispid; caudical leaves oblanceolate, denticulate to bipinnate, petiolate; cauline leaves elliptic, ovate, lanceolate or linear, sessile, auriculate, runcinate to deeply pinnatifid with linear lobes, \pm lacinate near the base; stem erect, branched above or from near base, branches strict, divaricate, decumbent or prostrate, few- or many-headed; peduncles somewhat thickened or inflated toward summit, the heads nodding or erect before anthesis; heads medium to large, many-flowered; involucre cylindric-turbinate to campanulate, the outer bracts linear to lanceolate, becoming lax, the inner bracts lanceolate, becoming strongly carinate or navicular, enclosing the marginal achenes, spongy-thickened toward base, pubescent on inner face; receptacle either densely ciliate or paleaceous with linear chartaceous paleae; flowers yellow, the ligules usually reddish-purple on outer face in marginal florets; achenes biform, the marginal (rarely absent in certain variants), stout, shortly and coarsely beaked or beakless, the inner longer, slender, finely beaked; pappus sordid white, 3–7 mm long, 2-seriate, persistent. Chromosomes, $2n = 10$.

W., central, and S. Europe to the Caspian Sea; Asia Minor, Syria, and N. Palestine, to Transcaucasia and W. Persia; seashore, plains, hills, and mountains, mostly at lower elevations but occasionally up to 2000 m altitude or even higher.

This polymorphic species or Rassenkreis includes very numerous forms which exhibit combinations of variations in several characters, such as habit, leaf dissection, glands on stem and involucre, glandless setae on involucre, relative length of outer and inner involucre bracts, size of florets and flower parts, size and color of achenes, length of pappus, and presence or absence of paleae on the receptacle. Many of these variations are genetic in nature, but many modifications in size, habit, and degree of development of certain characters are caused by environmental factors. Most notable among these are the occasional depauperate and repressed forms, which may be difficult to classify. There exist, however, three fairly distinct subspecies with different although overlapping areas of distribution (see fig. 212); and it is possible to identify nearly all the specimens of this species as one or another of these three subspecies. Certain variants, however, are obviously hybrids between the subspecies.

As an explanation of the origin and present status of this Rassenkreis or rheogameon, the following hypothesis has been proposed (Babcock, E. B., Jour. Bot. 76: 202–203, 1938): (1) Three closely related species were involved: *C. foetida* L. (including m.v. 2 and 3); *C. rhoadifolia* Bieb.; and *Rodigia commutata* Spr. (2) Preceding or during the period of differentiation of these species, they become geographically isolated: *C. foetida* in S.W. Europe; *C. rhoadifolia* in the Caucasus reg.; and *C. commutata* in Asia Minor. (3) All three spread until they met in W. Asia Minor or the Balkan Pen. and, through hybridization, gave rise to the intergrading forms connecting them. (4) Meanwhile each of the original species became polymorphic through mutation, so that many local races exist. (5) The combined result is an exceedingly variable complex of minor variants caused by gene mutations and intergrading forms resulting from hybridization. Thus, it becomes necessary to treat the three original species as subspecies of a single inclusive species. There is already good precedent for doing this with respect to *C. foetida* and *C. rhoadifolia*. The inclusion of *C. commutata* as a subspecies is supported both by study of specimens collected in the wild and by cytogenetic research. Regarding the origin of subsp. *rhoadifolia*, however, an alternative hypothesis is given on p. 695.

Key to the Subspecies of *Crepis foetida*

Receptacle ciliate but not paleaceous; pappus 4–7 (mostly 5–6) mm long.

Outer involucre bracts narrower, the longest mostly half (rarely two-thirds) as long as the inner; trichomes of the involucre mostly piliform, glandular.....145, *a. vulgaris*

Outer involucre bracts broader, the longest about two-thirds as long as the inner; trichomes of the involucre mostly setiform, eglandular.....145, *b. rhoeadifolia*

Receptacle paleaceous; pappus 3–4 mm long.....145, *c. commutata*

145, *a. Crepis foetida vulgaris* (Bisch.) Babc., Jour. Bot. 76: 205, 1938. Plant annual, rarely biennial or (m.v. 13) perennial (?), 0.3–7.5 dm high; involucre more narrowly campanulate than in subsp. *rhoeadifolia*, ratio of length to width 1.5 to 1.8 (average about 1.7); outer involucre bracts about $\frac{1}{2}$ or rarely $\frac{2}{3}$ as long as the inner, lanceolate, gradually and strongly attenuate upward; corolla 9–16 mm long; ligule 1–1.6 mm wide, dorsally pubescent toward base; teeth 0.1–0.6 mm long; corolla tube 3–7 mm long, pubescent with short 2–3-celled acicular hairs; anther tube about 3×1 mm dis.; appendages 0.4–0.5 mm long, narrow, acute or obtuse; filaments 0.6 mm longer; style branches yellow or sometimes greenish, 1.5–2 mm long, partly exerted at anthesis; marginal achenes 7–9 mm long, brown or dark brown, with an oblique dorsal scar just above the base, the beak paler, equal to, shorter, or longer than the body; inner achenes 12–17 mm long, brown; pappus 4–7 (mostly 5–6) mm long. Flowering May–Aug. See pls. 17, 18, c, and figs. 217, 218.

Crepis foetida L., Sp. Pl. 2: 807. 1753.

C. barbata Mill., Gard. Dict. ed. 8, n. 2, 1768, non L.

Pioris foetida Lamk., Fl. Fr. 2: 108. 1778.

Barkhausia foetida F. W. Schmidt, Samml. Phys. Aufs. 1: 283. 1795.

Wibelia graveolens Gaert. Mey. et Scherb., Fl. Wett. 3: 144. 1801.

Hostia foetida Moench, Meth. Suppl. 221. 1802.

C. interrupta Sibth., Fl. Graec. Prod. 2: 137. 1813.

B. graveolens Link, Enum. Hort. Berol. 2: 290. 1822.

C. foetens Link, ex Buch, Phys. Bes. Canar. 147. 1825, non DC.

C. glandulosa Guss., Pl. Rar. 329. t. 56. 1826, non Brot. ex DC.

B. glandulosa Presl., Fl. Sic. xxxi. 1826.

B. Candollei Spr., Syst. 3: 657. 1826.

B. prostrata Dumort., Fl. Belg. 61. 1827.

C. radicata S. et S., Fl. Graec. 7: 74. t. 800. 1833, non Forsk.

C. foetida B. occidentalis Webb et Berth., Phyt. Canar. 3: 458. 1836–1850.

B. saecynthia Marg. et Reut., ex DC., Prod. 7: 158. 1838.

C. insularis Moris. et Not., Mem. Acad. Torino 2: 85. t. 3(1). 1839.

C. graveolens Schrad., ex Steud., Nom. ed. 2, 1: 436. 1840.

Amisoderis foetida Fisch. et Mey., Ind. Sem. Petropol. 32. 1835–1842.

Wibelia foetida Sch. Bip., Cich. n. 64. 1841.

B. triangularis C. Koch, Linnaea 23: 686. 1850.

C. foetida a. vulgaris Bisch., Beitr. 252. 1851.

C. fallax Boiss., Fl. Orient. 3: 850. 1875.

Hieraciodes foetidum et *H. fallax* O. Kuntze, Gen. 1: 346. 1891.

B. supina Rouy, Fl. Fr. 9: 211. 1905.

B. gracilis Lej., ex Rouy, loc. cit.

C. foetida subsp. *eufoetida* Beger ex Domin, Preslia (Vest. Ceskoslov. Bot. Spol. Praz) 13–15: 252. 1935.

W., central, and S. Europe to Crimea; Aegean Archipelago, Greece, Crete, and Cyprus; Asia Minor, Syria, and S.W. Persia. Adventive in Algeria and Madeira, and in the Canary Is., where it has become naturalized.

The type is cited below as m.v. 1.

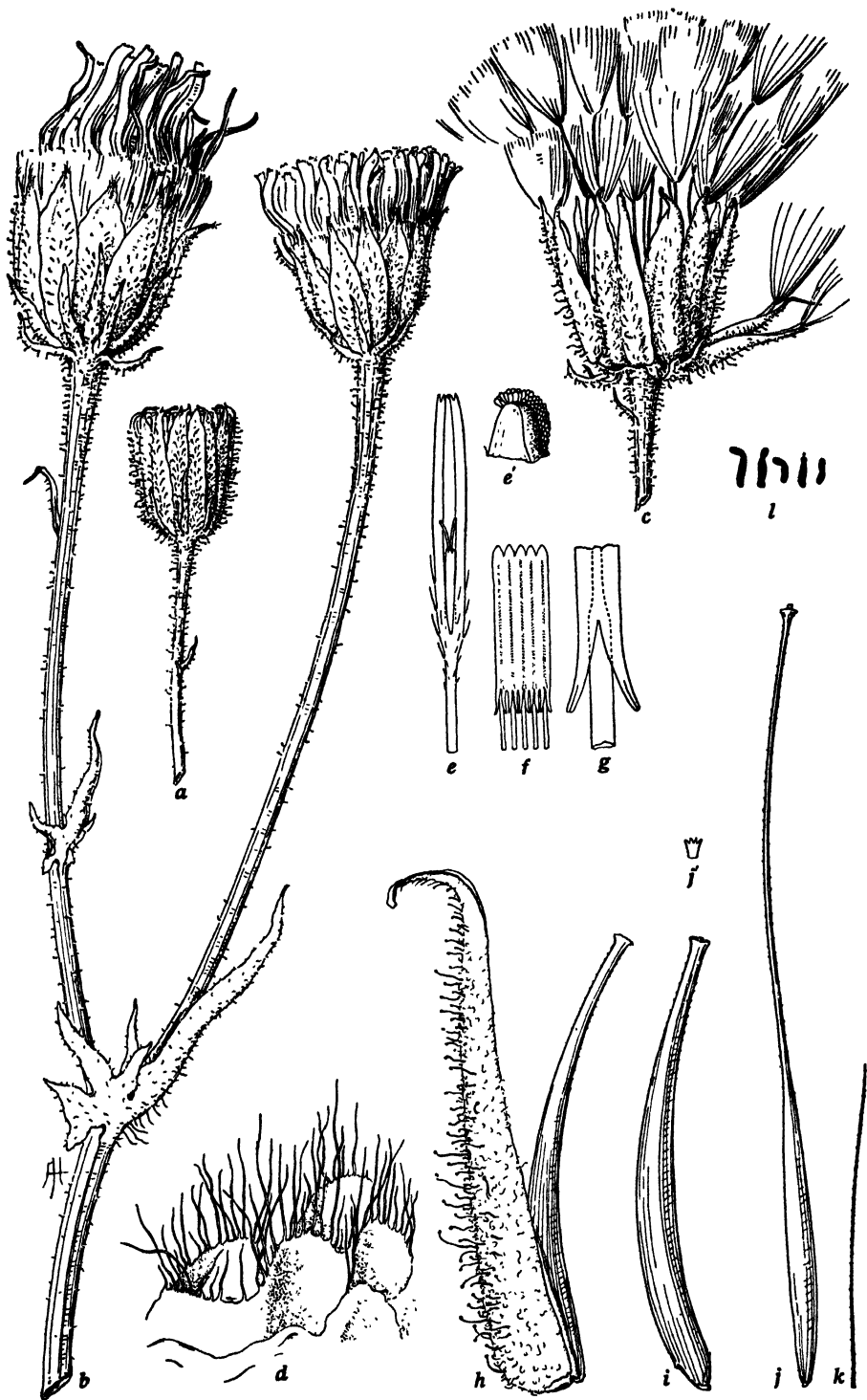


Fig. 217. *Creps foetida vulgaris*, typical, *a-k*, from hort. genet. Calif. 1812 (UC 669378); *l*, from hort. genet. Calif. 1751 (grown from seeds received from the Ghent Bot. Gard.; cf. UC 676610): *a-c*, heads, $\times 2$; *d*, detail of receptacle, $\times 25$; *e*, floret lacking ovary, $\times 4$; *e'*, detail of ligule tooth, $\times 25$; *f*, anther tube, $\times 8$; *g*, detail of appendages, $\times 32$; *h*, inner involucre bract with enclosed achene, $\times 8$; *i-k*, marginal and inner achenes, spicule from achene (enlarged), and a pappus seta, $\times 8$; *l*, somatic chromosomes, $n = 5$, $\times 1250$. Cf. pl. 17.

Canary Is.: Teneriffe, *Boivin 286* (DS); Teneriffe, near Giumar, *Bourgeau 450* (K) m.v. 3; Palma, near Tazacorte, Barranca de Las Angustias, *Pitard 242* (Mo) m.v. 34; Gomera, mountains above Hermigua, cult. Hort. Berol. (B) m.v. 37; La Caldera, La Banda, Arguel, *Lowe* in 1858 (K) m.v. 34; La Caldera, *Lowe* in 1858 (K) m.v. 35. **Spain:** Zaragoza, road to Calatayud, *Vicioso* in 1912 (Bar) m.v. 20; Leon, Villafranca del Biergo, *Lange* in 1852 (K, G); Valentino, Partitxol I., near Dianium, *Font Quer* in 1923 (Bar) m.v. 2; Balearic Is., Pont d'Inca, *Bianor-Marie* in 1917 (Bar); Sierra Nevada, 1200–1800 m, *Ball* in 1851 (G); Sierra Nevada, Horcajo de Freveles, 2400 m, *Font Quer* in 1923 (Bar) m.v. 10; Catalonia, Vilanajor, Montseny, *Gallard* in 1918 (Bar); Catalonia, Cabanas, *Sennen 427* (Bar, Ms, UC) m.v. 19; Catalonia, Vinaixa, 500 m, *Font Quer* in 1920 (Bar) m.v. 21; Catalonia, Martorell de la Selon, *Font Quer* in 1920 (Bar) m.v. 21; Gerona, La Sellera i Sant Julia del Lhor, Conca de Ter, n. 345 (Bar) m.v. 20. **France:** ex descr. (L) type = m.v. 1; Haute-Garonne, Toulouse, Cours de l'arsenal, *Munby* in 1857 (K); Gard, Pont-du-

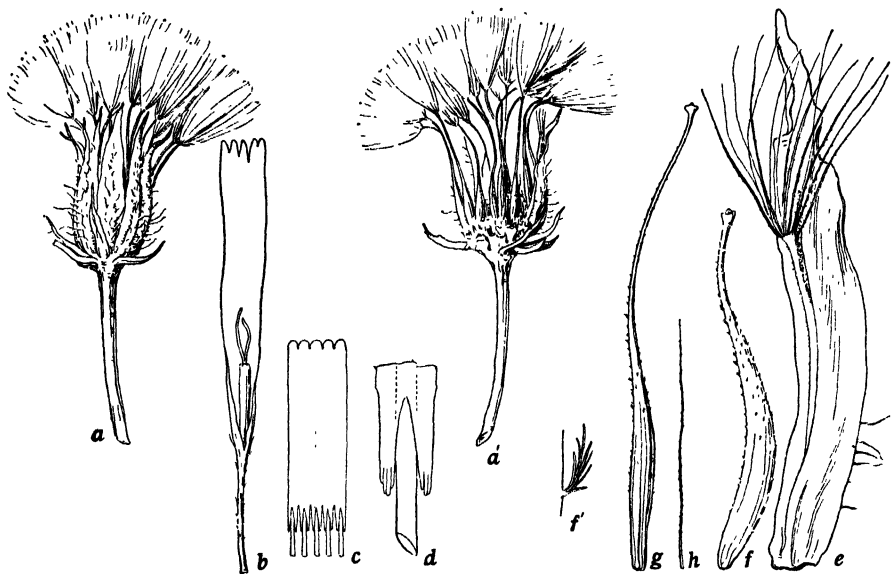


Fig. 218. *Crepis foetida vulgaris*, from type of *C. fallax* Boiss. (Bo): a, head, $\times 2$; a', same, with bracts removed and showing achenes and cilia on receptacle, $\times 2$; b, floret lacking ovary, $\times 4$; c, anther tube, $\times 8$; d, detail of appendages, $\times 32$; e-h, inner involucre bract enclosing achene, together with marginal and inner achenes, spicule from achene (enlarged), and a pappus seta, $\times 8$. Cf. pl. 18, c.

Gard, *Hall 12474* (UC); *ibid.*, *Hall 12473* (UC) m.v. 19; Puy-de-Dome, near Clermont Ferrand, *Pellat* in 1867 (Grenoble); Seine et Oise, Fremigni, in 1813, ex herb. J. Gay (K); Seine, near Paris, La Varenne-Saint-Maur, *Puel and Maille* in 1847 (G); Valois, Thury, in 1819 (DS) m.v. 33; Vaucluse, Carpentras, in 1860, ex herb. Mill (K); Var, Toulon, hills near Clairet, *Bourgeau* in 1848 (K) m.v. 5; Burgundy, Dijon, *Fleurot* in 1834 (DC) m.v. 10; Isère, near Grenoble, Rochefort, *Pellat* in 1899 (Grenoble); Lorraine, Nancy, *Lussene* in 1829 (DS). **England:** Berkshire, Maidenhead, in 1847 (K) m.v. 33; Kent, Dartford, *Linton* in 1885 (Minn). **Germany:** Hamburg, Dampfurth, Wandsbek, *Kausch* in 1894 (UC) m.v. 23; Sax-Weimar, Jena, *Steele* in 1886 (Po); Anhalt, Bernburg, *Matthies* in 1902 (Po); Pfalz, Speyer, 100 m, *Eigner* in 1906 (G); Saxony, Saalkreis, Trebitz, *Matthies* in 1900 (Minn); Thuringia, Erfurt, *Rudolph* in 1886 (Minn); Thuringia, *Wallroth* in 1834 (DC) m.v. 11; Palatinate, fields between Gönheim and Ellerstadt, *Schultz 64* (K, G) m.v. 33; Palatinate, Ellerstadt, *Schultz 97* (K) m.v. 46. **Switzerland:** Geneva, Salève, *Boissier* (K); Valais, St. Leonard, *Favrat* in 1864 (K); Douanne, Jura, Cernois, *Butté* in 1878 (K). **Italy:** Liguria, Busalla, ex herb. Ball (G) m.v. 22; Ischia I., "Lava del Arso," *Spencer* in 1904 (G) m.v. 10; Naples, 1358 (DC); Sicily, *Gussone* in 1829 (DC) m.v. 2; Sicily, *Gussone* in 1831 (DC) m.v. 3; Sicily, *Gussone* (Naples) m.v. 2 and 3; Sicily, *Gussone* (UC) m.v. 3; Sicily, Palermo, hills and mountains, *Ross 158* (K, Munich, G) m.v. 2 and 3; Sardinia, Maddelana I., *Vaccari* in 1897 (Bur) m.v. 14; Corsica, near Sari-de-Portovecchio, Mt. Santa, 600 m, *Briquet* in 1911 (Bur) m.v. 14; Corsica, Capraja I., dry places, cala delle Leccie, *Moris and Notaris* (Tor) m.v. 24. **Austria:** S. Tirol, Riva, Lake Benaca, 80–200 m, *Porta 3414*

(K, G, Minn); S. Tirol, Artzwang, *Eggers* in 1902 (Minn). Yugoslavia: Carniola, Laibach, Krain, *Fleischmann 2532* (K, G, Po); Bosnia, Travnik, *Sendtner 359* (Munich) m.v. 13. Albania: sandy seashore near Salina, *Baldacci* in 1894 (K) m.v. 40. Greece: *Druce* (Oxford) m.v. 14; *Deest* in herb. Sibth. (Oxford ?) m.v. 13; *Zuccarini* (Munich) m.v. 13; ex hort. genet. Calif. 2047, 2048, cult. from seeds collected by *Frangos* in 1927 (UC) m.v. 13; Mt. Hymetti, 60–300 m, *Orphanides 342* (K, Munich, G, Mo) m.v. 14; Theodoras Scala, Lithochovi, *Halacsy 1339* (UWH) m.v. 14; Thessaly, Pharsala, *Hausknecht* in 1889 (K) m.v. 17; Thessaly, Kalabaka, *Hausknecht* in 1889 (K) m.v. 17; Attica, *Boissier* in 1862 (K) m.v. 5; Athens, Phaleri and Lykabettum, *Hausknecht* in 1885 (K) m.v. 2; Athens, *Heldreich 2281* (G) m.v. 2; Zante I., *Margot* in 1837 (DC) m.v. 5; Corfu I., *Coreyrae*, *Sagburg* in 1890 (UWH); Crete, Khamistika dist., *Baldacci 79* (UWH) m.v. 14. Cyprus: Galatia, *Sintenis and Btgo* in 1880 (K) m.v. 18. Russia: Crimea and adjacent regions, *Lewillé* (B). Turkey: Anatolia, Brusa, *J. Ball* in 1867 (K) m.v. 13; Brusa, Yalova, *Krause 4444* (UC) m.v. 48; Trebizond, *Koch* (B) m.v. 12; Kurdistan, *Sintenis 1333* (K) m.v. 15; Cilicia, Anamour, *Peronin 80* (Bo) m.v. 48; Mersina, *Balansa 651* (K, G) m.v. 16. Syria: Aleppo, *Kotschy 178* (G) m.v. 2; Musairy Mts., Masian, *Haradjian 3408* (DL) m.v. 13; Liban, Ehden, *Kotschy 268* (K) m.v. 36; Tripoli, *Blanche* (G) m.v. 39. Turkey, Syria, or Iraq: Euphrates R., *Frey 2315* (B) m.v. 43. Persia: Bushire (Buschir, Abuschehr), fields and wadies, *Stapf* in 1885 (K) m.v. 42; Khane Radar, *Stapf* in 1885 (K) m.v. 42.

Minor Variants of C. foetida vulgaris

1. (*C. foetida* var. *typica* Hal., Consp. Fl. Graec. 2: 216. 1902.) (Pl. 17, b, c.) Annual; stem erect, rather slender, branched above or below the middle, branches strict, elongated; heads medium; involucre cylindric-campanulate, the gland hairs mostly rather short; corolla about 9 mm long; anther tube about 3 mm long; style branches yellow; achenes brown; marginal achenes about 8 mm long, subterete, gradually attenuate into a coarse paler beak; inner achenes about 13 mm long, with a long fine paler beak; pappus 5–6 mm long. Most of the specimens cited under subsp. *vulgaris* are of this form or close to it unless otherwise designated. The type of Linnaeus was (ex descr.) collected in France.

2. (*C. foetida vulgaris* f. *glandulosa* [Guss.] Bab., Jour. Bot. 76: 205. 1938; *C. glandulosa* Guss., loc. cit.; *Barkhausia glandulosa* Presl., loc. cit.; *C. foetida* B. *occidentalis* b. *australis* Webb et Berth., Phyt. Canar. 3: 458. 1836–1850; *C. glandulosa* var. *simplex* et var. *interrupta* Haussk., Mitt. Thüring. Bot. Ver. 7: 53. 1895.) Annual; stem erect, rather stout, the branches short, 1–3-headed; stem, peduncles, and involucre gland-pubescent; corolla about 12 mm long; style branches yellow; marginal achenes 8–9 mm long, with a coarse beak equal to body; inner achenes 12–16 mm long. In Sicily, the type region, this form apparently occurs at higher elevations, whereas the next is found at lower levels. These two variants are illustrated by the specimens of Ross (pl. 17), both of which were collected in June, 1899, and distributed under the same number. The two plants of m.v. 2 were just coming into flower; the other, m.v. 3, was in fruit. *Ross 158A*, 158B (Munich, G), mountain near Palermo, Sicily; *Font Quer* in 1923 (Bar), Portitxol I., Valencia or Alicante, Spain; *Heldreich 2281* (G) Athens, Greece; *Hausknecht* in 1885 (K), Phaleri and Lykabettum, Athens, Greece (this last collection contains 5 depauperate specimens; cf. m.v. 24); *Kotschy 178* (G), Aleppo, Syria (a reduced state of this variant).

3. (*C. foetida vulgaris* f. *pinnatifida* [DC] Bab., Jour. Bot. 76: 205. 1938; *C. glandulosa* B. *pinnatifida* DC, Prod. 7: 158. 1838.) Annual, stem erect, robust, branched from near base, branches long, stiffly erect, with several large heads on rather long peduncles; corolla up to 16 mm long; style branches yellow; marginal achenes 8–9 mm long, with a coarse beak equal to body; inner achenes 12–15 mm long, strongly spiculate. This variant and the last are fairly distinct, especially in the abundance of gland hairs on the stems, the long corollas and marginal achenes, and the numerous outer bracts of the involucre; but in all these characters intergrading forms occur. This particular variant, however, is of special interest because of its resemblances to subsp. *rhoeadiifolia* (q.v.). *Gussone* ex herb. Guss. (UC), Silene, Sicily; *Ross 158C* (Munich, G), hillsides near Palermo, Sicily; ex herb. Parlat. (K), Sicily; ex hort. genet. Calif. 2307, cult. from seeds ex Hort. Bot. Palermo (UC), Sicily.

4. (*C. foetida vulgaris* f. *candollei* [Spr.] Bab., Jour. Bot. 76: 205. 1938; *Barkhausia Candollei* Spr., loc. cit.; DC, Prod. 7: 158. 1838.) Leaves oblong, rather wide, sinuate-dentate. The two folios in herb. DC contain only cultivated plants. Original habitat unknown.

5. (*C. foetida vulgaris* f. *zacynthia* [Marg. et Reut.] Bab., Jour. Bot. 76: 206. 1938; *Barkhausia zacynthia* Marg. et Reut., loc. cit.) Stem low, erect, slender, glandular, usually few-branched above the middle, with oblanceolate denticulate dentate or runcinate-pinnatifid leaves. Apparently a reduced state of m.v. 2. *Margot* in 1837 (DC), Zante I., Greece; *Boissier* in 1862 (K), Attica, Greece; *Bourgeau* in 1848 (K), Clairet, near Toulon, France.

10. (*C. foetida vulgaris* f. *gracilis* [Lej.] Bab., Jour. Bot. 76: 206. 1938; *Barkhausia gracilis*

Lej., *loc. cit.*) Plant about 1 dm high; stem very slender, 1-2-headed; caudical leaves up to 3 cm long, 0.8 cm wide; heads small. *Fleurot* in 1834 (DC), Dijon, France; *Font Quer* in 1923 (Bar), 2400 m, Horcajo de Freveles, Sierra Nevada, Spain; *Spencer* in 1904 (G), volcanic sand, Ischia I., Italy.

11. Many-stemmed from the swollen caudex; stems 1-3-branched; branches pedunculate, long, slender, arcuate; cauline leaves very small, linear. The habit resembles that of certain low, diffuse forms of *C. capillaris*, as in m.v. 11 of that species, and, like some of these, it may be the result of mutilation. Probably this is *Barkhausia pinguis* Rehb., ex Moesl. Handb. ed. 2, 2: 1411. 1828. *Wallroth* in 1834 (DC), Thuringia, Germany.

12. (*C. foetida vulgaris* f. *triangularis* [C. Koch] Babe., Jour. Bot. 76: 206, 1938; *Barkhausia triangularis* C. Koch, *loc. cit.*) Biennial (or perennial ?); stem short, many-branched; branches elongated, spreading, few-headed; caudical leaves cinereous, setulose. *Koch* (B, type), Trebizond, Armenia.

13. (*C. foetida vulgaris* f. *interrupta* [Sibth.] Babe., Jour. Bot. 76: 206. 1938; *C. interrupta* Sibth., *loc. cit.* et Fl. Graec. 9: t. 803, 1837, non DC.) Annual, rather low; stem diffusely branched, branches ascending; caudical leaves lyrate, irregularly pinnately parted; stems, peduncles, and involucre hispid with glandless setae; involucre bracts and style branches intermediate between subsp. *vulgaris* and subsp. *rhoeadifolia*; anther tube and appendages sometimes as in the latter. *Deest* in herb. Sibth. (Oxford ?), Greece; *Frangos* in 1927, ex hort. genet. Calif. 2047, 2048 (UC), Greece; *Zuccarinus* (Munich) Greece; *Sendtner* 359 (Munich), near Travnik, Bosnia; *Haradjan* 3408 (DL), near Masian, 600-800 m, Musairy Mts., Syria; *Ball* in 1867 (K), Brusa, Turkey.

14. (*C. foetida vulgaris* f. *radicata* [S. et S.] Babe., Jour. Bot. 76: 206. 1938; *C. radicata* S. et S., *loc. cit.*; *Barkhausia radicata* in Godr., Mem. Acad. Sci. Monspel. sec. med. 1: 436. 1853, *fid.* Thell., Fl. Adven. Montpell. 581. 1875; *C. glandulosa* Guss. var. *maritima* Boiss., ex Haussk., Mitt. Thüring. Bot. Ver. 7: 54. 1895.) Biennial or perennial; root often long; caudex swollen; stems numerous, semidecumbent, 1-3-branched, branches long, slender, arcuate, pedunculate or few-headed; caudical leaves short, runcinate-pinnatifid; heads and florets typical. *Orphanides* 342 (K, Munich, G, Mo), Mt. Hymetti, Attica, Greece; *Halacsy* 1339 (UWH), Lithochovi Theodhras Scala, Greece; *Druce* (Oxford), Greece; *Baldacci* 79 (UWH), Khamistika dist., Crete; *Patten* 77 (G), Kavousi reg., Isthmus of Hierapetra, Crete; *Vaccari* in 1897 (Bur), Maddalena I., Sardinia; *Briquet* in 1911 (Bur), Mt. Santo, Corsica.

15. Resembles m.v. 14, but much reduced; caudical leaves 2-5 cm long; stems 5-7 cm high; involucre about 10 mm long; heads and florets typical. *Sintenis* 1333 (K), Kurdistan, Turkey.

16. Resembles m.v. 9 (p. 696) in habit, but more slender; outer involucre bracts intermediate in length, black at apex; involucre hairs absent or only a few short gland hairs present; corolla 12 mm long; style branches pale green; marginal achenes pale brown, 5.5 mm long; inner achenes brown, 8.5-10 mm long, the body slightly compressed, 0.5 mm wide, strongly attenuate to the small base; pappus 4-5 mm long. *Balansa* 651 (K, G), sandy seashore, Mersina, Cilicia, Turkey.

17. Stems very slender, reddish, branched from near base, branches arcuate, few-headed; involucre in fruiting heads about 10 mm long, finely gland-pubescent; corolla 10-12 mm long; style branches green; marginal achenes 6 mm long, pale brown or gray; inner achenes 10-12 mm long, pale brown. *Haussknecht* in 1889 (K), Kalabaka and Pharsala, Thessaly, Greece.

18. Outer involucre bracts more as in subsp. *rhoeadifolia* and involucre both gland-hairy and setose with long rather coarse glandless setae; corolla about 11 mm long; style branches yellow; marginal achenes 6 mm long, brown with coarse pale beak; inner achenes 9-12 mm long, dark brown with paler beak. *Sintenis and Rigo* in 1880 (K), vineyard near Galatia, Cyprus.

19. Tall and slender with only 1-3 heads; leaves denticulate. The habit probably results from crowding. *Sennen* 427 (Bar), as *C. foetida* var. *subintegrifolia* Lgc.; *ibid.*, (Ms, UC), Cabanas, Catalonia, Spain; *Hall* 12473 (UC), Pont-du-Gard, France.

20. Stem and leaves more like those in m.v. 3; stem tall, robust, reddish, diffusely branched; leaves bipinnately divided; involucre and floral characters typical. *Vicioso* in 1912 (Bar), near Calatayud, Spain; collector ?, no. 345 (Bar), Conca del Ter, Girona, Spain.

21. Like m.v. 2 in habit; stem reddish, sparsely and finely hispid; leaves canescent, densely hispid; involucre glandular; corolla about 8 mm long; style branches yellow; marginal achenes about 6.5 mm long; inner achenes 10-12 mm long. *Font Quer* in 1920 (Bar), Martorell de la Selon, Catalonia, Spain; *Font Quer* in 1918 (Bar), Poblet, Catalonia, Spain; *Font Quer* in 1920 (Bar), Vinaixa, Catalonia, Spain.

22. Plants low; leaves bipinnate; stem and leaves hispidulous with fine glandless hairs; involucre hairs fine, long and short, glandless; outer involucre bracts intermediate in length between subsp. *vulgaris* and subsp. *rhoeadifolia*; corolla 12-14 mm long; corolla tube about 6 mm long; style branches green. *Ex herb. J. Ball* in 1890 (G), Busalla, Liguria, Italy.

23. Like m.v. 19 in habit, leaves, and color of stems; peduncles and involucre gland-pubescent; style branches greenish. *Kausch* in 1894 (UC), Wandsbek, Dampfurth, Hamburg, Germany.

24. (*C. foetida vulgaris* f. *insularis* [Moris. et Not.] Babe., Jour. Bot. 76: 206. 1938; *C. insularis* Moris. et Not., loc. cit.) Much reduced; leaves dentate; stem simple, 1-headed; involucre gland-pubescent or villous; style branches yellow. *Moris and Notaris* (Tor), dry places, cala delle Leccie, Capraja I., Corsica.

29. (*C. foetida vulgaris* f. *prostrata* [Dumort.] Babe., Jour. Bot. 76: 206. 1938; *B. prostrata* Dumort., loc. cit.; *C. foetida* var. *diffusa* Lej. et Court., Comp. 3: 110. 1836; *C. prostrata* Dumort., ex Michot, Fl. du Hain, 254. 1845, fide Wildeman et Durand, Prod. Fl. Belg. 2: 810. 1899.) Not seen by me. Has gland-pubescent on involucre ex deser.

31. (*C. foetida vulgaris* f. *supina* [Rouy] Babe., Jour. Bot. 76: 206. 1938; *B. supina* Rouy, loc. cit.) Plant canescent; stems 0.8–1.5 dm long, decumbent or prostrate but not filiform, 2–8-headed; leaves small; involucre like that in subsp. *vulgaris*, but white-hairy. Not seen by me. Reported to occur along borders of fields, Ampus, Var, France.

33. Involucres nearly devoid of gland hairs; those which do occur are very short and hidden among the numerous long glandless hairs; otherwise typical. *Schultz* 64 (K, G), Palatinate, Germany; collector ♀ in 1819 (DS), Thury en Valois, France.

34. Resembles m.v. 2 except in pubescence of the stem, which consists of long and short glandless setae, with some gland hairs on the peduncles. *Lowe* in 1858 (K), Arguel, La Banda, La Caldera, Canary Is.; *Pitard* 242 (Mo), Barranco de Las Angustias, near Tazacorte, Palma, Canary Is.

35. Resembles m.v. 3, except in pubescence of the stem, which consists of short fine glandless hairs with a few glands on the peduncles. *Lowe* in 1858 (K), La Caldera, Canary Is.

36. Intermediate between m.v. 14 and 15; plant 1.5 dm high; caudical leaves 5 cm long, 1.3 cm wide; stem 3-branched at base, the branches slender, diffuse, stiffly semierect, 2–3-headed, sparsely hispidulous near base, glabrous above; heads, florets, and achenes typical, except that the inner achenes have a prominent yellow basal callus. *Kotschy* 268 (K), field near Ehden, 1515 m, Liban, Syria.

37. (*C. foetida vulgaris* f. *gomerea* [C. Bolle] Babe., Jour. Bot. 76: 206. 1938; *C. foetida* var. *gomerea* C. Bolle, Bonpl. 8: 135. 1860.) A cultivated form of subsp. *vulgaris*. Ex Hort. Berol. (B), grown from seeds collected in mountains above Hermigua, Gomera, Canary Is.

39. Outer involucre bracts like those in subsp. *rhoeadifolia*, and style branches dark green; plant low; caudical leaves small, lyrate, runcinate-pinnatifid; stems few, 9 cm high, 1–2-headed; heads rather small; outer bracts sparsely hispid; inner bracts sparsely pubescent with short glandular and medium glandless hairs; corolla about 9 mm long; achenes and pappus like those in m.v. 48. Probably a hybrid derivative. *Blanche* (G), Tripoli, Syria.

41. Marginal achenes elongated and similar in color to the inner; similar to m.v. 48 in both size and habit of plant and in shape and pubescence of leaves; corolla about 11 mm long; anther tube about 3 mm long; marginal achenes 6.5 mm long, the beak rather coarse, equal to body, strongly spiculate; inner achenes dark brown, up to 9 mm long, finely beaked; pappus 5 mm long. This form, like the preceding, shows resemblance to *C. foetida commutata* in the elongated marginal achenes and in other characters, and it may be a hybrid derivative. *Stapf* 160 (K), margins of fields and wadies around Bushire, "also on the naphtha springs near Daleki, plentiful on a wet place at the foot of Kotel Pach-i-gachi," S.W. Persia.

42. Low, with delicate fastigiate branches and 6–8 small heads; leaves denticulate; involucre sparsely pubescent with long fine yellow gland hairs; corolla 9–10 mm long; anther tube about 2.5 mm long; marginal achenes, as in m.v. 48, 5.5 mm long; inner achenes up to 9 mm long, finely beaked; pappus 4.5 mm long. Perhaps another hybrid derivative. *Stapf* in 1885 (K), hills near Khane Radar, "also at Komary and in a more hairy form in the Kasrun valley," S.W. Persia.

43. Plant with the general appearance of m.v. 48; leaves glabrescent; outer involucre bracts and achenes typical of subsp. *vulgaris*. *Freyn* 2315 (B), steep stony place on Euphrates R., Turkey, Syria, or Iraq.

45. Intermediate between this subspecies and subsp. *rhoeadifolia* in pubescence of stem and involucre and in the achenes; plant fairly robust with long branches spreading from near base; stem, branches, and peduncles hispid with long glandless setae; outer bracts short, hispidulous; inner bracts gland-pubescent with long and short, rather coarse hairs; marginal achenes brown, 7 mm long, with very short coarse beak; inner achenes brown, up to 11.5 mm long; pappus 6.5 mm long. *Radde* (K), Caucasus.

46. Heads more like those in subsp. *rhoeadifolia*; involucre bracts mostly glandless; and marginal achenes yellowish, more like those in subsp. *rhoeadifolia*; length of outer bracts as in subsp. *vulgaris*; corolla 10–12 mm long; style branches greenish. Another plant of the same collection (in Herb. Po) is typical subsp. *rhoeadifolia*. The specimen cited here is probably the result of natural hybridization between the two subspecies. *Schultz* 97 (K), grassy place near Ellerstadt, Palatinate, Germany.

48. (*C. foetida vulgaris* f. *fallax* [Boiss.] Babe., Jour. Bot. 76: 206. 1938; *C. fallax* Boiss., loc. cit.; *Hieraciodes fallax* O. Kuntze, loc. cit.) (Pl. 18, c. Fig. 218.) Annual, about 4 dm high; leaves

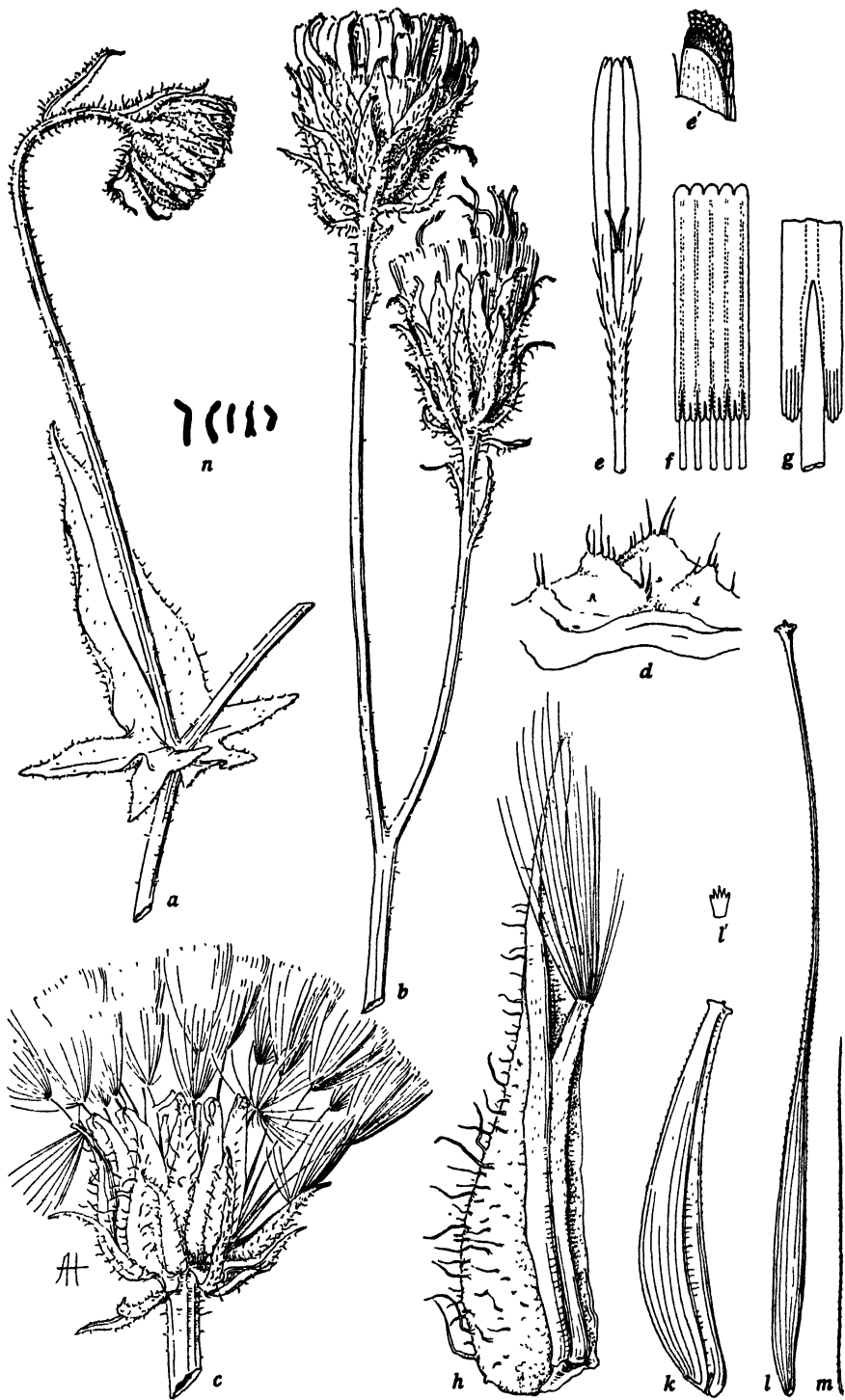


Fig. 219. *Crepis foetida rhoeadifolia*, a-d, h-m, from hort. genet. Calif. 28.2318-2, 9 (UC 669379); e-g, from hort. genet. Calif. 28.1534-5 (UC 669378); n, from hort. genet. Calif. 28.2188 (UC 676612): a-c, heads, $\times 2$; d, detail of receptacle, $\times 25$; e, floret lacking ovary, $\times 4$; e', detail of ligule tooth, $\times 25$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, bract enclosing achene, $\times 8$; k-m, marginal and inner achenes, spicule from achene (enlarged), and a pappus seta, $\times 8$; n, somatic chromosomes, $n = 5$, $\times 1250$. Cf. pl. 18, a, b.

pinnately parted, the lower ones petiolate, the middle cauline sessile, subamplexicaul, the upper linear or bractlike; stem erect, branched from below middle, branches long, remotely forked, bearing several heads on long peduncles; involucre like that in typical subsp. *vulgaris* but rather small; outer bracts about $\frac{1}{2}$ as long as the inner, glabrous or sparsely pubescent; corolla 9–14 mm long; anther tube about 3 mm long; style branches 2 mm long, yellow; marginal achenes 6 mm long, brown with paler beak equal to body and finer than in typical subsp. *vulgaris*; inner achenes 8–12 mm long; pappus 4–5 mm long. Closely resembling and often confused with subsp. *commutata*, this variant may have originated through hybridization. *Peronin 80* (Bo type of *C. fallax*), sea-shore and mountains near Anamour, Cilicia, Turkey.

145, b. *Crepis foetida rhoeadifolia* (Bieb.) Schinz et Keller, Kr. Fl. Schweiz, ed. 3, 361. 1914. Plant annual, 1–7 dm high; involucre broadly campanulate at maturity, ratio of length to width 1 to 1.5 (average about 1.3); outer involucre bracts about $\frac{2}{3}$ as long as the inner, broadly lanceolate, rather abruptly narrowed to the obtuse ciliate tip, like inner bracts \pm hispid with pale glandless setules; corolla 11–19 mm long; ligule about 2 mm wide; teeth 0.2–0.5 mm long; corolla tube 4–6 mm long, pubescent with short 2–3-celled acicular hairs; anther tube about 4×1.25 mm dis.; appendages 0.5–0.7 mm long, oblong, acute or obtuse; filaments 0.8 mm longer; style branches dark green or sometimes light green or yellow, up to 3 mm long, partly exerted at anthesis; marginal achenes 5–7 mm long, pale brown or brownish-gray, with a very short coarse beak and oblique dorsal scar just above the base; inner achenes 12–16 mm long, brown or light brown; pappus 5–7 mm long. Flowering June–Sept. See pl. 18 and fig. 219.

Crepis rhoeadifolia Bieb., Fl. Taur. Cauc. 3: 537. 1819.

Barkhausia rhoeadifolia Fisch. et Mey., Ind. Sem. Petropol. 4: 32. 1835–1942.

C. foetida A. *orientalis* Webb. et Berth., Phyt. Canar. 3: 458. 1836–1850.

C. bysantina DC., Prod. 7: 158. 1838.

C. echinoides Ledeb., Ind. Sem. H. Dorpat 23. 1821; Fl. Ross. 2: 819. 1844.

C. rodigioides Sch. Bip., ex Koch, Linnaea 23: 687. 1850.

C. rhoeadifolia var. *genuina* Koch, Linnaea 23: 685. 1850.

C. foetida var. *hispidula* Bisch., Beitr. 252. 1851.

C. Strybrnyi Velen., Fl. Bulg. 333. 1891.

C. foetida var. *subdivisa* Schur, Verh. Naturf. Brünn 36: 208. 1897.

C. Nestmeiri F. Herm. et Deg., Magyar Bot. Lapok. 32: 64. 1933.

Asia Minor, Kurdistan, and N.W. Persia; Transcaspiian Prov., Transcaucasia, S. Russia; the Balkan Pen. southward into N. Greece; eastward into central Europe.

The type of this subspecies has not been seen by me, but the original description and numerous corroborative ones are sufficient to establish its identity.

Two hypotheses concerning the origin of this subspecies have been suggested (B. and Cave: 155–156). First, the progenitors of the group of forms included here may have developed as a distinct species in the Caucasus reg. (just as *C. eritreensis* and *C. Thomsonii* developed in their isolated regions) and later spread into Asia Minor and S.E. Europe, meeting and hybridizing with subsp. *commutata* and subsp. *vulgaris*. Second, subsp. *rhoeadifolia* may have originated through hybridization between subsp. *commutata* and subsp. *vulgaris*, especially with m.v. 2 or m.v. 3, perhaps in N. Asia Minor, and then spread around the Black Sea into S. Russia and eastward. Although the former alternative may appear at first to be more reasonable, yet there are several reasons for considering the second hypothesis also tenable. These include evidence from morphological and physiological characters, such as the occurrence of palea-like structures in certain plants of subsp. *rhoeadifolia*, evidence on hybrid fertility, inheritance of paleae in hybrids between subsp. *commutata* and subsp. *rhoeadifolia*, the variability in self-sterility within subsp. *rhoeadifolia*, and the occurrence of variants of this subspecies with low genetic fertility.

Turkey: Constantinople, *Aucher-Eloy 3451* (DC) m.v. 7; Black Sea coast, between Midia and Ormanlı, near Tschalingos Bay, *Hermann* in 1927 (Hermann) m.v. 47; Bithynia, Dardanelles, *Sintenis 692* (K) m.v. 8; Bosphorus, *Krause 418* (UC); Ismid, *Powers 36* (PA); Brusa, *Krause 4159* (UC); between Modania and Brusa, in 1862, ex herb. Mill (K) m.v. 8; Pontus, Samsun, *Krause 3904* (UC); Trebizond, Gumushe Hane, *Balls 758a* (UC); Phrygia, Afyoun-Kavahisar, *Krause 3477* (UC) m.v. 28; Galatia, Cankaya, near Ankara, *Krause 3656* (UC); Lycaonia, Ak Shehr (Akschehir) *Bornmüller 5220* (K) m.v. 8; Cappadocia, Simas, *Krause 3732* (UC); Lycia, Elmali, *Bourgeau 170* (K, Ms) m.v. 8; Cilicia, Taurus Mts., Bozanti, *Eig and Zohary* in 1931 (UC); Bulgardagh, Birdiglek, *Eig and Zohary* in 1931 (UC); between Bozauli and Ak-Köprin bridge, *Eig and Zohary* in 1931 (UC, G) m.v. 26; Kurdistan, *Stapf 894* (K) m.v. 8; *ibid.*, *Sintenis 1333* (K) m.v. 15; Orfa (Urfa), *Haussknecht* in 1865 (K) m.v. 8. **Armenia:** Aimec-Cogas, *Sintenis 6201A* (K); *ibid.*, *Sintenis 6201B* (K) m.v. 6. **Cyprus:** Stroumbi, near Paplos, *Haradjian 764* (DL) m.v. 7 or 8. **Syria:** Musairi Mts., Ain-Halskim, *Haradjian 2050* (DL) m.v. 8; Amanus Mts., between Aintab and Haruniji, *Haradjian 3548* (DL) m.v. 8; Mt. Cosmis, *Haradjian 3010* (DL) m.v. 7; Aleppo, *Kotschy 178* (K) m.v. 9; Afrin R., road to Aleppo, *Haradjian 4363* (K) m.v. 9; Killis, *Haradjian 4508* (K) m.v. 8; Liban, *Cedrus* forest above Bsherre, 1800–1900 m, *Zohary* in 1931 (UC) m.v. 9. **Persia:** Tabriz, *Gilliat-Smith 1760* (K). **U. S. S. R.:** Transcasian Prov., near Ashkabad, Keshi, *H.A.* in 1930 (UC); Transcaucasia, ex hort. genet. Calif. 1534, cult. from seeds sent by *Woronoff* in 1922 (UC); Tiflis, ex hort. genet. Calif. 1618, 2188, 2316, 2318, cult. from seeds sent by *Navashin* (UC); Caucasus, *Radde* (K) m.v. 45; Crimea, near Baksan, *Halacsy 662* (K); Ukraine, Odessa, ex herb. Benthams (K); *ibid.*, *Nordmann* in 1846 (K) m.v. 8. **Bulgaria:** Sliven, *Schneider 393* (K); *ibid.*, *Schneider 393* (Mo) m.v. 44; Satirja, *Schneider 1416* (K); Varna dist., *Gilliat-Smith 807* (K); Budapest, *Borbas* in 1878 (G); Sofia, *Tamadjev* in 1932 (UC). **Rumania:** Bessarabia, Tyram, *Lundaman* in 1846 (Po). **Greece:** Macedonia, Vaden, *Adamovic* in 1903 (K); Thessaly, Pindus Mts., Mt. Zygos, above Malakasi, *Miss Topali 14* (UC); Mt. Olympus, *Gutol* in 1932 (UC). **Albania:** Upper Albania, *Grisebach* (Mo); Salina, seashore, *Baldacci* in 1894 (K) m.v. 40. **Czechoslovakia:** Prag, *Ruprecht* (Mo); Brünn (Brno), *Schur 2351* (K) m.v. 30; Biela, *Wiedemann 980* (G). **Austria:** Vienna, Grinsing, *Halacsy 324, 3415, 1151* (K, G, Minn, Mo). **Germany:** Palatinate, Ellerstadt, *Schultz 97* (Po) m.v. 46. **Switzerland:** Vaud, Orbe R. basin, Ependes, *Moehrlen* in 1890 (RB).

Minor Variants of C. foetida rhoeadifolia

6. Habit and leaves of m.v. 5 (p. 691); involucre sparsely setose, the setae coarse, yellow. *Sintenis 6201B* (K), Aimec-Cogas, Armenia.

7. (*C. foetida rhoeadifolia* f. *byzantina* [DC.] Babe., Jour. Bot. 76: 207. 1938; *Barkhausia byzantina* DC., loc. cit.) Stem robust, remotely branched from near base, branches long, ascending, 1–3-headed; peduncles short; involucrel setae medium to coarse, glandless; marginal achenes pale yellow; inner achenes pale brown, more gradually attenuate than usual, the beak stramineous. *Aucher-Eloy 3451* (DC) Constantinople.

8. The whole plant hispid with coarse yellow glandless setae; stem robust, branched above middle or near summit; leaves oblanceolate, dentate or runcinate-pinnatifid; inner involucrel bracts ventrally pubescent with coarse yellowish hairs; corolla 8.5–14 mm long; style branches usually yellow; achenes as in m.v. 7. Very distinct in habit, in the coarse involucrel setae, and in the pale yellowish color of leaves and involucre. See m.v. 32, which is similar but has glands on involucre. *Bourgeau 170* (K, Ms), Elmali (Elmali), Lycia, Turkey; *Bornmüller 5220* (K), Ak Shehr, Galatia, Turkey; *Haradjian 4508* (K), Killis, Syria; *Haussknecht* in 1865 (K), Orfa, Kurdistan, Turkey; *Mill* in 1862 (K), between Mudania and Brusa, Bithynia, Turkey; *Sintenis 692* (K), Dardanelles, Turkey; *Nordmann* in 1846 (K), Odessa, Ukraine.

9. (*C. foetida rhoeadifolia* f. *rodigioides* [Sch. Bip.] Babe., Jour. Bot. 76: 207. 1938; *Barkhausia rodigioides* Sch. Bip., loc. cit.) Plant rather low, diffusely few-branched from near base; branches long, 1–4-headed; habit like that in m.v. 48 (p. 693); involucrel setae medium, glandless and finely glandular; inner involucrel bracts with rather coarse white or yellow hairs on inner face; receptacle ciliate; corolla 12–13 mm long; style branches yellow or pale green; mature achenes lacking in first two specimens cited; in *Zohary's* plant marginal achenes 5–7.5 mm long, brown, narrow, short-beaked; inner achenes 10–13 mm long, pale brown, with a delicate yellow beak and much expanded pappus disk; pappus 5–6 mm long, white. *Kotschy 178* (K), Aleppo, Syria; *Haradjian 4363* (K), Afrin R., road to Aleppo, Syria; *Zohary* in 1931 (UC), *Cedrus* forest above Bsherre, Liban, Syria.

25. (*C. foetida rhoeadifolia* f. *echioides* [Ledeb.] Babe., Jour. Bot. 76: 207. 1938; *C. echioides* Ledeb., loc. cit.; = ? *B. foetida* var. *hirta-scabra transilvanica* Schur, Verh. Naturf. Brünn 36: 208. 1897.) Said by Ledebour to be a larger, more hirsute form of *C. foetida rhoeadifolia*. See m.v. 8.

26. Plants 1–3 dm high; heads small; involucre in fruiting heads 8–10 mm long; marginal

achenes 4–5 mm long; inner achenes 7–8 mm long; pappus 5 mm long. *Eig and Zohary* in 1931 (UC, G), about 850 m, between Bozauli and Ak-Köprün bridge, Bulgar Dag, Cilicia, Turkey.

27. (*C. foetida rhoeadifolia* f. *hispidissima* [Koch] Bab., Jour. Bot. 76: 207. 1938; *B. rhoeadifolia* var. *hispidissima* Koch, loc. cit.) Not seen by me. Described as more robust than the typical form and the whole plant white-hairy. See m.v. 8.

28. Receptacle paleaceous, as in subsp. *commutata*; achenes more like those in subsp. *rhoeadifolia*, but the marginal ones slender and definitely beaked. The two plants in this collection are like subsp. *rhoeadifolia* in size, habit, leaves, heads, and indumentum, and the style branches are pale green. But the strongly paleaceous receptacle and slender marginal achenes show the effects of hybridization with subsp. *commutata*. These may be chance segregates from a mixed population or they may represent a stable race. *Krause 3477* (UC), overgrown land near Afyon-Karalisar, Phrygia, Turkey.

30. (*C. foetida rhoeadifolia* f. *subdivisa* [Schur] Bab., Jour. Bot. 76: 207. 1938; *Barkhausia foetida* var. *subdivisa* Schur, loc. cit.; said to be intermediate between subsp. *vulgaris* and subsp. *rhoeadifolia*; probably identical with *B. foetida* var. *foliis minus divisa* Fisch. et Mey., Ind. IV Sem. H. Petropol. 32. 1835.) Tall, robust, leafy, few-branched above; lower leaves dentate, middle leaves runcinate-pinnatifid, upper leaves denticulate and lacinate at base; peduncles short; heads like those in subsp. *rhoeadifolia*. *Schur 2351* (K), near Brünn, Czechoslovakia.

32. (*C. foetida* var. *assyriaca* Bornm., Bull. Herb. Boiss. ser. 2, 7: 436. 1907; *C. foetida* var. *glandulosa* [Guss.] ex Bornm., loc. cit.; *C. foetida commutata* f. *assyriaca* Bab., Jour. Bot. 76: 207. 1938.) Not seen by me. Ex descr., it resembles m.v. 8, but in addition has gland hairs on the involucre; heads broad, many-flowered; involucre bracts thick and densely setose with yellow spreading glandless setae sometimes 4 mm long. Kurdistan and N.W. Persia.

38. (*C. foetida rhoeadifolia* f. *strybrnyi* [Velen.] Bab., Jour. Bot. 76: 207. 1938; *C. Strybrnyi* Velen., loc. cit.; *C. foetida* var. *Strybrnyi* Stefanoff, in litt.) Not seen by me. Ex descr., intermediate between subsp. *rhoeadifolia* and subsp. *vulgaris* m.v. 48; resembling the latter in the small heads and narrow acuminate outer bracts of the involucre; resembling the former in the long glandless involucre hairs. Grassy plains of Sadovo, Philippopolis, Bulgaria.

40. Outer involucre bracts intermediate toward subsp. *vulgaris*; style branches yellow; and marginal achenes elongated; plants 1.5–2.5 dm high, slender, with reduced leaves, heads few, rather large; involucre pubescent with rather short yellowish glandless hairs; corolla about 14 mm long; anther tube about 3.5 mm long; marginal achenes nearly equal to the bracts, body elongated, beak short; inner achenes up to 14 mm long; pappus 6–7 mm long. *Baldacci* in 1894 (K), sandy sea-shore near Salina, Albania.

44. Receptacle ± paleaceous; i.e., the receptacle has the alveolar surface and ciliate fimbrillae typical of subsp. *rhoeadifolia*, but some of the fimbrillae are prolonged at one point into a palea-like structure which is also ciliate. Although the paleae in subsp. *commutata* are not ciliate, the occurrence of these palea-like structures in these plants indicates the close connection between the two subspecies. *Schneider 393* (Mo), vineyard near Sliven, Bulgaria.

47. (*C. foetida rhoeadifolia* f. *Nestmervi* [F. Herm. et Deg.] Bab., Jour. Bot. 76: 207. 1938; *C. Nestmervi* F. Herm. et Deg., loc. cit.) Perennial, 1.3–2.5 dm high; leaves 8 cm long, 2 cm wide; stem branched from middle or near base, branches erect or arcuate, 1–5-headed; involucre about 12 mm high, 7 mm wide in fruit; longest outer bracts about $\frac{3}{4}$ as long as the inner and, like them, glabrous or sparsely setose, glandless; corolla 13 mm long; anther tube 3.3×1.25 dis.; style branches 2.25 mm long, yellow; marginal achenes 6.5 mm long, narrow, subterete, coarsely beaked; inner achenes 8.5–10 mm long; pappus 5–6 mm long. The rather low stature, glabrescent foliage and involucres, yellow style branches, and narrow marginal achenes indicate resemblance to m.v. 48 (p. 693). The perennial habit is thought by Hermann to be due probably to suppression by plants of other genera, such as *Epilobium*, since apparently perennial (and sometimes glabrate) plants of otherwise typical subsp. *rhoeadifolia* were found on the near-by grassy seashore. *Hermann* in 1927 (Hermann, UC) on the projecting ledges and summits of calcareous rocks, up to 30 m alt., bounding Tschalingos Bay on the south, Black Sea coast between Midia and Ormanlı; *Hermann* in 1927 (Hermann, UC), rocks enclosing Tschalingos Bay on the north, European Turkey.

145. *c. Crepis foetida commutata* (Spr.) Bab., Jour. Bot. 76: 207. 1938. Plant annual, 1–4 dm high; involucre campanulate, never reflexed in fruiting heads, 8–11 mm high, 5–7 mm wide, strongly setose with long yellow glandless setae, densely pubescent with short fine gland hairs, glands yellow or purple; outer bracts 12–20, longest $\frac{1}{2}$ as long as the inner, lance-linear, acute, becoming indurate, persistent; inner bracts 12–16, lanceolate, acute or obtuse at the ciliate apex; receptacle paleaceous, with two paleae subtending each achene, paleae free or united at base, linear,

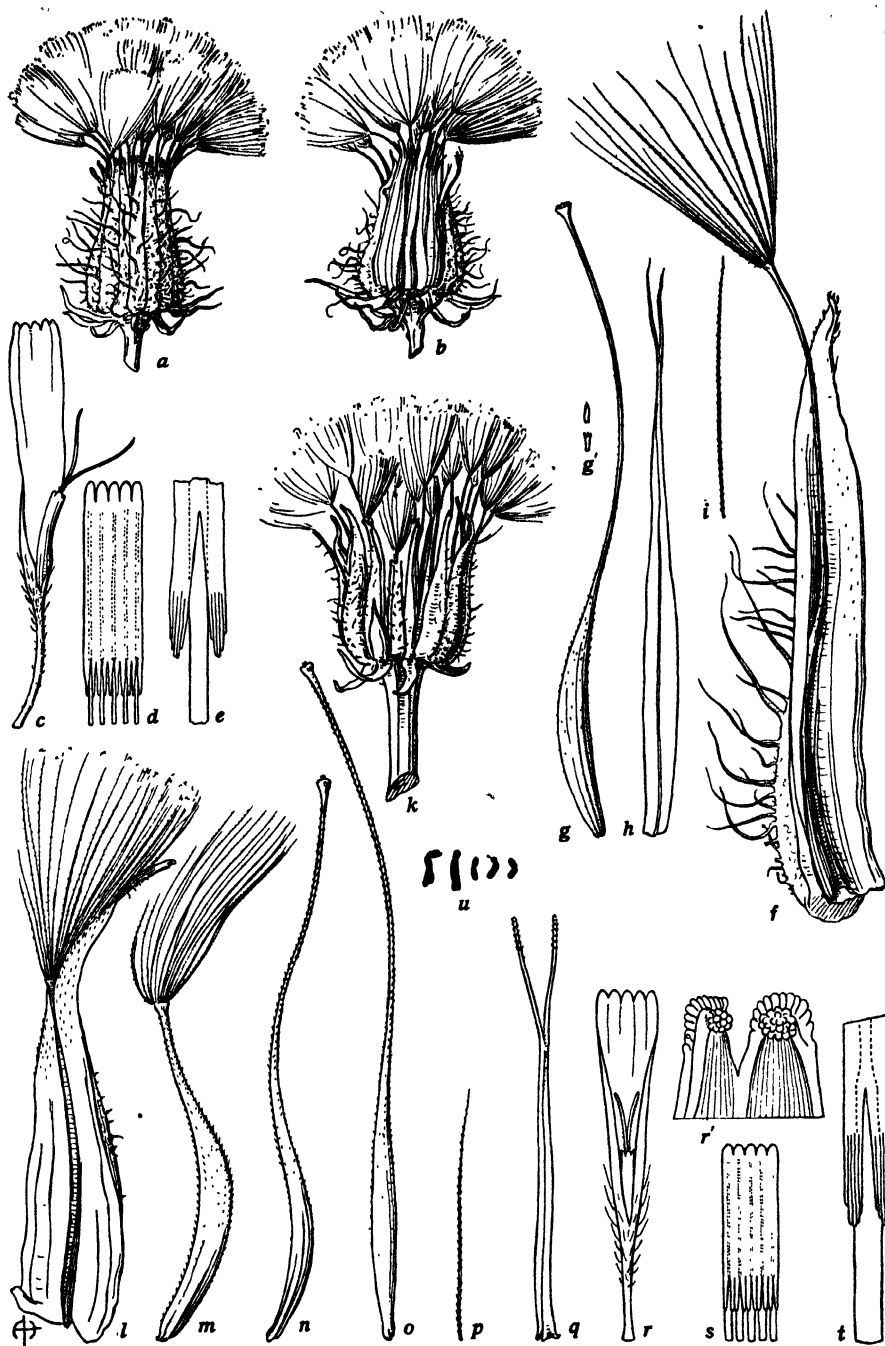


Fig. 220. *Crepis foetida commutata*, a, b, f-i, from Haradjian 1989a (DL); c-e, from Bornmüller in 1910 (Weimar, as *C. brachypappa* Bornm.); k-q, m.v. 52, from Fairchild in 1930, Lesbos I. (UC 429433); r-t, from progeny of Fairchild's plant, ex hort. genet. Calif. 31.2970-3 (UC 519491); u, from hort. genet. Calif. 2219 (grown from seeds collected in Greece): a, head, $\times 2$; b, same, with bracts removed and showing achenes and paleae but no cilia on receptacle, $\times 2$; c, floret lacking ovary, $\times 4$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f-i, inner involucre bract enclosing achene, inner achene, spicules from same (enlarged), palea, and pappus seta, $\times 8$; k, head, $\times 2$; l, bract enclosing achene, $\times 8$; m-o, a marginal and 2 inner achenes, $\times 8$; p, q, pappus seta and palea, $\times 8$; r, floret lacking ovary, $\times 4$; r', detail of ligule teeth, $\times 25$; s, anther tube, $\times 8$; t, detail of appendages, $\times 32$; u, somatic chromosomes, $n = 5$, $\times 1250$.

white or pale yellow, chartaceous, gradually attenuate into a pale brown simple or furcate awn, nearly equal to the achenes; corolla 12–18 mm long; ligule 1.7–2 mm wide; teeth 0.2–0.5 mm long; corolla tube 4–5 mm long, pubescent with several-celled acicular hairs up to 1.5 mm long; anther tube (3)4 × 1 mm dis.; appendages 0.5–0.6 mm long, oblong, acute or obtuse; filaments 0.3–0.5 mm longer; style

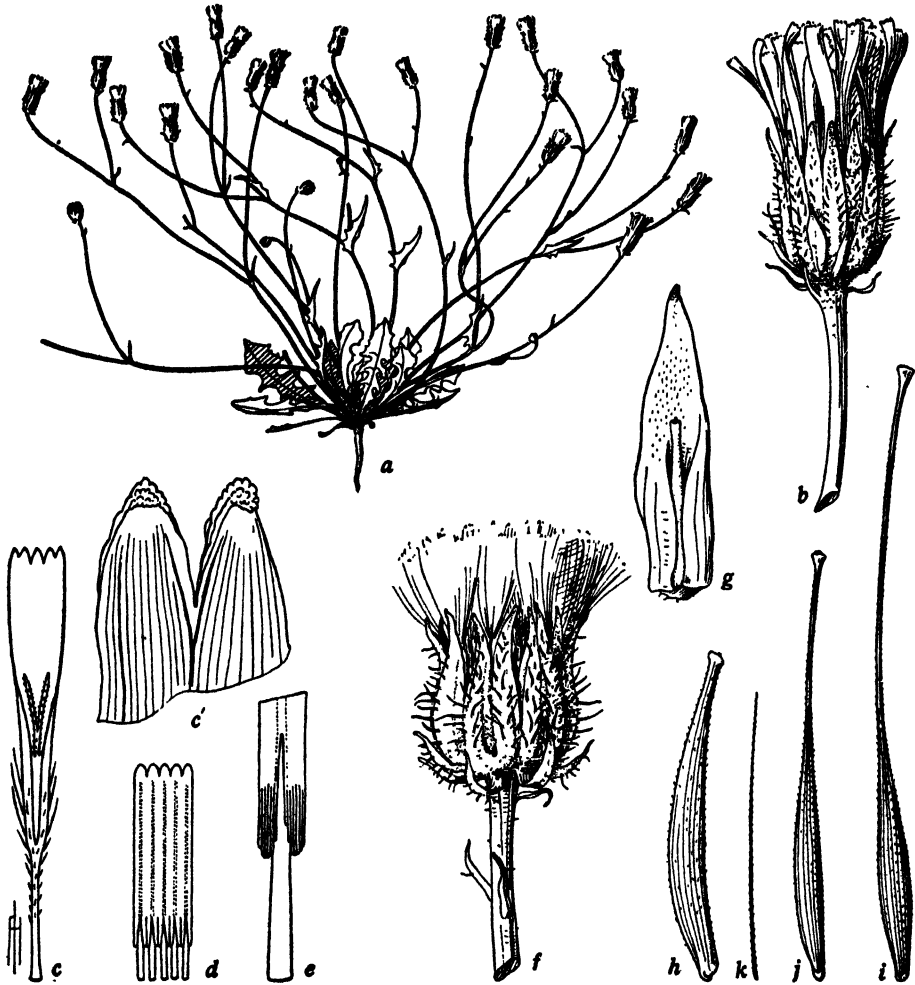


Fig. 221. *Crepis foetida commutata*, m.v. 49, from Sintenis 4391 (Lund, as *Rodigia gracilis* F. et S.): *a*, plant, $\times \frac{1}{4}$; *b*, flowering head, $\times 2$; *c*, floret lacking ovary, $\times 4$; *d*, detail of ligule teeth, $\times 50$; *e*, anther tube, $\times 8$; *f*, detail of appendages, $\times 32$; *g*, inner involucre bract, inner face, $\times 4$; *h-k*, 3 achenes and a pappus seta, $\times 8$.

branches 2–2.75 mm long, yellow, sometimes fully exserted; marginal achenes (sometimes lacking) gray, tawny, or brown, 5–9.5 mm long, laterally compressed, with oblique basal scar, dorsally ribbed, ventrally pale, \pm pubescent, attenuate into a coarse beak; inner (or all) achenes pale or dark brown, 10–14 mm long, body 2.5–4 mm long, fusiform, 10-ribbed, attenuate into a slender or very fine beak 3–5 times as long as body; pappus 3–4 mm long. Flowering Apr.–June. See pl. 18, *d* and figs. 220, 221.

Rodigia commutata Spr., Neu. Entd. 1: 273. 1820.
Seriola commutata Less., Syn. 131. 1832.

Phalacroderis coa DC., Prod. 7: 97. 1838.

Barkhausia hirta Koch, Linnaea 23: 687. 1850.

E. bulgarica Velen., Fl. Bulg. 362. 1891.

B. gracilis Freyn. et Sint., Oest. Bot. Zeit. 64: 259. 1894.

Crepis brachypappa Bornm., Beih. Bot. Centralbl. 32: 418. t. 19, 1914.

The type of this subspecies has not been seen by me, but its identity is beyond question.

N.E. Mediterranean reg. from Crete northward through E. Greece and the Aegean Archipelago to S. Bulgaria; Asia Minor and N. Syria eastward to W. Persia.

Although subsp. *commutata* was first described as a genus because of its paleaceous receptacle, the occurrence of fertile natural hybrids with subsp. *rhoeadifolia* in Asia Minor (see m.v. 28, 55, and 56) indicates the close relationship of these two entities. Experimental crosses between subsp. *commutata* and various strains of both of the other subspecies have produced some hybrids with high fertility, some with low fertility, and some sterile ones. Certain variant forms of this subspecies have been given names by earlier authors. These and certain others are included in the list of numbered variants below.

Crete: near Phaestos, *Guiol 1278* (UC); near Canea, *Malaxa Mts.*, ex hort. genet. Calif. 31.2864, cult. from seeds collected by *Babcock* in 1930 (UC). **Rhodes:** near the city, *J. Ball 2450* (US); ex hort. genet. Calif. 28.1666, cult. from seeds sent by *Pampanini* (UC). **Mytilene** (Lesbos): *Filia* and *Karioniri*, *Fairchild* in 1930 (UC) m.v. 52. **Greece:** *Corinthia-Argolis*, *Nauplia*, *Costopulos* in 1931 (UC); near *Argos*, *Babcock 323* (UC) m.v. 51. **Bulgaria:** E. *Rhodope Mts.*, *Ortakjoi*, *Stefanoff* in 1923 (UC) m.v. 50; *ibid.*, *Achtaroff* in 1932 (UC) m.v. 50. **Turkey:** *Bosporus*, *C. Koch* (B) as *B. hirta*; *Pontus*, *Tonia*, *Sabadja*, *Sintenis 4391* (Lund) m.v. 49; *Pontus*, near *Turtsal*, *Krause 3792, 3812* (UC) m.v. 55; *Ankara*, near *Etlik*, *Krause 4352* (UC) m.v. 56; *Phrygia*, *Usak*, *Krause 3437* (UC); *Cilicia*, *Kalouver*, *Peronin 49* (P. Genoa). **Syria:** between *Hammah* and *Aleppo*, *Haradjan 1989* (DL); between *Kerkhan* and *Alexandretta*, *Zohary* in 1931 (UC); between *Telejin* and *Abudhur*, *Zohary* in 1931 (UC); near *Homs*, *Zohary* in 1931 (UC) m.v. 53. **Persia:** Mt. *Noa-Kuh* and *Kercuo* in Mt. *Kuh-i-Marab*, *Bornmüller* in 1910 (Weimar) as *C. brachypappa*.

Minor Variants of *C. foetida commutata*

49. (*C. foetida commutata* f. *gracilis* [Freyn et Sint.] Babe., Jour. Bot. 76: 207. 1938; *Rodigia gracilis* Freyn et Sint., loc. cit.) Plant large; habit spreading; marginal achenes only 5.25 mm long, strongly attenuate but not beaked. *Sintenis 4391* (Lund), plain, *Sabadja*, *Tonia*, *Pontus*, *Turkey*.

50. (*C. foetida commutata* f. *bulgarica* [Vel.] Babe., Jour. Bot. 76: 207. 1938; *Rodigia bulgarica* Vel., loc. cit.; *E. commutata* var. *bulgarica* [Vel.] Stoj. et Stef., in herb.) Plants less robust and spreading than m.v. 49, but nearly twice as large as m.v. 53; involucre bracts tomentose but almost devoid of setae and gland hairs; receptacular paleae more numerous than in typical subsp. *commutata*, the additional ones pseudosetiform; marginal achenes 5.5–7 mm long, very shortly beaked; inner achenes 10–13 mm long. A transitional form between this and typical subsp. *commutata* was reported from *Thrace* by *Stefanoff* (*Nicolov* in 1913 in Herb. Sofia). The statement of *Velenovsky* that there are two types of paleae on the receptacle in these plants is inaccurate. Each normal palea is accompanied by 1–5 similar ones arising from the same base. The extra paleae are often so narrow as to simulate setae, but they are always flat and chartaceous toward the base. It is probable that the peculiar features of this form are conditioned by two or more genes. *Stefanoff* in 1923 (UC), dry limy soil, *Ortakjoi*, E. *Rhodope Mts.*, *Bulgaria*; *Achtaroff* in 1932 (UC), among grass, "Wogto," above *Ortakjoi*, *Bulgaria*.

51. Plants robust, less spreading or strictly erect; heads rather small; marginal achenes about 5 mm long, shortly beaked; inner achenes 10–14 mm long, the body 2.5–3 mm long; pappus 3–4 mm long. *Babcock 323* (UC) gravelly beach near *Kios*, 8 km from *Argos*, *Corinthia-Argolis*, *Greece*; *Costopulos* in 1931 (UC), *Mycenae*, *Corinthia-Argolis*, *Greece*.

52. Plants low even in cultivated specimens, cf. hort. genet. Calif. 31.2970 (UC); caudical leaves up to 9 cm long; stems up to 1.5 dm high; heads rather small, in the smallest plants somewhat resembling those of *C. setosa*, but paleae and achenes like those in subsp. *commutata*, except smaller, also with a tendency toward reduction in the indumentum of the involucre; marginal achenes pale brown, 6.5 mm long, beak equal to body, strongly spiculate, inner achenes up to

13 mm long, body 3 mm long, dark brown, the beak pale, spiculate from base to apex; pappus 4.5 mm long. *Fairchild* in 1930 (UC), Filia and Karioniri, Mytilene (Lesbos) I., Aegean Archipelago, Greece. (Fig. 221.)

53. Dwarfish even under cultivation, cf. hort. genet. Calif. 32.3165, 1-7 (UC); heads larger than in m.v. 52, more as in typical subsp. *commutata* and with no reduction of the indumentum; achenes of different wild plants rather variable in size; marginal achenes 5-8 mm long, shortly beaked; inner achenes 8-11.5 mm long, body 2.5-3 mm long; pappus 3-3.5 mm long. *Zohary* in 1931 (UC), environs of Homs, Syria.

54. (*C. foetida commutata* f. *coa* [DC.] Bab., Jour. Bot. 76: 207. 1938; *Phalacroderis coa* DC., loc. cit.) Depauperate; plant only 0.9 dm high; leaves few, up to 3 cm long, 0.5 cm wide; stem very slender, 3-branched from near base, 3-headed; heads small; involucre 6.5 mm high, 3-4 mm wide in fruit; corolla 9 mm long; achenes (immature) 5 mm long, beaked; pappus 2-2.5 mm long; paleae linear near base, awnlike above, equal to involucre. These notes agree with de Candolle's description and with Boissier (Fl. Orient. 3: 880. 1875). *d'Urville 190b* (K, when seen by me this diminutive specimen was mounted on the same sheet with an isotype of *C. Fontiana*), summit of Cos (= Cos I.), Dodecanese, Aegean Archipelago, Greece.

55. Involucral indumentum sometimes like that in subsp. *rhoeadifolia*, sometimes like that in subsp. *commutata*, sometimes very sparse; receptacle alveolate, ciliate, cilia sometimes long, merging into paleae, true paleae also present but reduced to setiform; style branches green. Although variable in size, the 6 plants collected by Krause resemble subsp. *commutata* in size and habit as well as in size and shape of the mature heads and size and shape of the leaves. They may represent a population that will become more stable for a combination of characters from the two subspecies. From the small size of the plants and their parts it does not seem likely that they are amphidiploid derivatives. *Krause 3792, 8812* (UC), stony slopes near Turtul, Pontus, Turkey.

56. Caudex rather strong and woody; style branches pale green; achenes more like those in subsp. *rhoeadifolia*; pappus 6 mm long. The one plant in this collection resembles subsp. *commutata* in size, habit, leaves, heads, and indumentum. It is probably a hybrid derivative. *Krause 4352* (UC), near Etlik, Ankara, Turkey.

Comparison of Cultivated Strains

Many accessions of this species have been grown in connection with our investigations. During the summer of 1928, 50 different strains were grown in the same garden at Berkeley under closely similar conditions. Some of these had been recently received from various botanic gardens and were more or less variable within the strains. Others were uniform strains secured by selection and self-pollination of individual plants during several years. There were also 10 strains grown from original seed collected from wild plants. Comparative notes were taken on all of the above strains. These, together with similar data obtained from more recently grown strains, from hybridization experiments, and from an extensive study of herbarium specimens, furnish the basis for the present treatment of this species. The complete data are too extensive for presentation here. Some of the statistical and other comparative data on 10 strains grown from wild seed and one botanic garden strain are presented in table 17. In part A of this table are presented the data on 4 strains of subsp. *vulgaris*; part C contains comparable data on 4 strains of subsp. *rhoeadifolia*; and part B gives the data on 3 strains representing 2 variants of subsp. *vulgaris*. It will be noted that, although there is some variation in the quantitative characters, the strains of both subspecies exhibit a high degree of uniformity and that, as represented by these strains, the two subspecies differ significantly in the thirteen compared characters. It is clear, however, that the two variants of subsp. *vulgaris* represented by the strains in part B are intermediate between the two subspecies in certain characters, such as length of corolla, length of style branches, and, in one of them, the bract ratio. There are many other intermediate forms between the two subspecies, most of which probably resulted from natural crossing in overlapping areas. Numerous experiments on crossing all three subspecies have been made, and the F_1 hybrids were usually intermediate in quantitative characters. When such hybrids are fertile, there is, in F_2 , Mendelian segregation

TABLE 17
STATISTICAL COMPARISON OF CERTAIN STRAINS OF CREPIS FORTIDA GROWN AT BERKELEY, CALIFORNIA, IN 1928
(All measurements in millimeters)
A. Subsp. vulgaris, from seed of wild plants

Accession number	Region of source	No. of plants	Mean height of plants	Mean diameter of open head	Mean length of corolla	Style branches		Hairs on involucre		Bract ratio I : O†	Stem color	Achene‡	
						Color	Mean length	Size	Glands*			Outer	Inner‡
1236	N. Italy	5	148	15.7	9.8	yellow	1.1	fine	+	2.5	green	8.5 brown	16 brown
1449	S. France ...	4	168	20.5	11.5	yellow	1.5	fine	±	2.4	green	6 brown	12 brown
1536	Transcaucasia	8	217	16.0	12.0	yellow	1.0	medium	±	2.1	green	9.5 brown	17 brown
1812	S. Spain	7	251	22.1	12.9	yellow	2.2	fine medium	+	2.2	green	8.5 brown	15 brown
Means of means			196	18.6	11.6		1.5			2.3		8.1	15

B. Subsp. vulgaris, 2047, 2048, m.v. 13, from seed of wild plants; 2307, m.v. 3, from seed from Palermo Botanic Garden

2047	Greece	8	185	26.3	14.7	yellow	2.4	medium	—	1.7	green	7 brown	13.5 brown
2048	Greece	7	136	25.5	13.7	yellow	2.1	medium	—	1.7	green	7 brown	14 brown
2307	Sicily	10	307	32.2	17.2	yellow	2.8	short, fine long, medium	+	2.1	green, little red	9.7 brown	17.5 brown

C. Subsp. rhoeadifolia, from seed of wild plants

1534	Transcaucasia	5	305	33.4	17.4	dark green	3.1	medium coarse	—	1.5	purple	(?)	(?)
1618	Tiflis	10	318	29.5	15.7	dark green	2.8	coarse	—	1.6	purple	6 pale	16 brown
2316	Tiflis	5	754	38.8	18.8	dark green	3.3	medium coarse	—	1.5	dark purple	6 pale	12 lt. brown
2318	Tiflis	9	538	34.8	17.4	dark green	2.9	medium coarse	—	1.4	dark purple	5.5 gray	12.5 lt. brown
Means of means			579	34.2	17.3		3.0			1.5		5.8	13.5

* Glands present indicated by +; absent, by —.

† I : O = length of inner divided by length of longest outer bracts.

‡ Data from several achenes on one or two plants of each strain.

§ Inner achenes vary in length in same head; these measurements were made on longest ones in each head.
|| Mature achenes not available.

of certain characters. One such segregating character difference is nodding versus erect position of the young flower heads before anthesis. Strains of these two types occur in both of these subspecies. (See also B. and Cave: 124–160.)

Phylogenetic Relations

As was shown by Babcock and Cave (*op. cit.*), the data from comparative morphology, cytogenetics, and geographic distribution all indicate that *Crepis foetida*, *sen. lat.*, together with *C. eritreënsis* and *C. Thomsonii*, had a monophyletic origin. It may be assumed that the ancestral stock had paleae on the receptacle and that the plants were self-compatible, since these are presumably more primitive characters than are absence of paleae and self-incompatibility. None, probably, of the existing species and subspecies in this group represents the ancestral type; i.e., all have become differentiated, some retaining self-compatibility, and one, subsp. *commutata*, keeping paleae on the receptacle while becoming differentiated, after isolation from its closest relatives, by gene mutations preventing self-compatibility. The assumed ancestral stock was probably distributed in Iran and Asia Minor, which are central with reference to the 3 outlying regions, Eritrea, India, and S.W. Europe.

Within the ancestral stock which produced these three species, differentiation probably was accomplished through gene mutations, with natural selection and geographic isolation playing important roles. Among the numerous gene mutations involved in the process of differentiation, those causing absence of paleae and self-incompatibility were evidently significant. Through these and other gene mutations two divergent lines arose. One of these led to the present-day group of forms known as *C. foetida commutata*. The other broke up into the many variants comprising *C. foetida vulgaris*, of which m.v. 1 and 2 are outstanding (fig. 222).

Of these two variants of *C. foetida vulgaris*, m.v. 2 appears to be more primitive because of its tall stature, robust habit, larger heads, and the combination of self-compatibility with the tendency for the flower heads to remain open in sunlight, in which respect it resembles *C. foetida commutata*. Minor variant no. 2 now occurs only in Sicily and at a few other isolated points in the Mediterranean and in Syria. It appears to be a relic form, whereas the typical form of subsp. *vulgaris* is an aggressive form which has become widespread in S. Europe.

The problem of the origin of *C. foetida rhoeadifolia* is interesting, there being two plausible hypotheses. The contention that the group of forms included in this subspecies may have developed as a distinct species in the Caucasus region and spread into Asia Minor and S. Europe was mentioned above. But *C. foetida rhoeadifolia* may have originated through hybridization between subsp. *commutata* and subsp. *vulgaris*, m.v. 2 or m.v. 3, perhaps in central or N. Asia Minor and then spread around the Black Sea and into S. Europe. There are several reasons for considering its origin through hybridization as tenable. First, *C. foetida rhoeadifolia* has been shown (B. and Cave, 127–132) to combine certain morphological and physiological features found in m.v. 2 and in *C. foetida commutata*. The occurrence of palea-like structures on the receptacle in certain plants of subsp. *rhoeadifolia* is particularly suggestive, although this and all the other characters held in common can also be attributed to a common origin with subsp. *commutata*. Second, the relations between subsp. *rhoeadifolia* and subsp. *commutata* with respect to hybrid fertility (B. and Cave, *op. cit.*, 134) can be interpreted in terms of the hybrid origin of subsp. *rhoeadifolia*. Apparently it is intermediate in its hybrid fertility relations between subsp. *vulgaris* and subsp. *commutata*. Third, the data on inheritance of paleae in hybrids between subsp. *rhoeadifolia* and subsp. *commutata* indicate a unique genetic basis for this character in the former (B. and Cave, *op. cit.*,

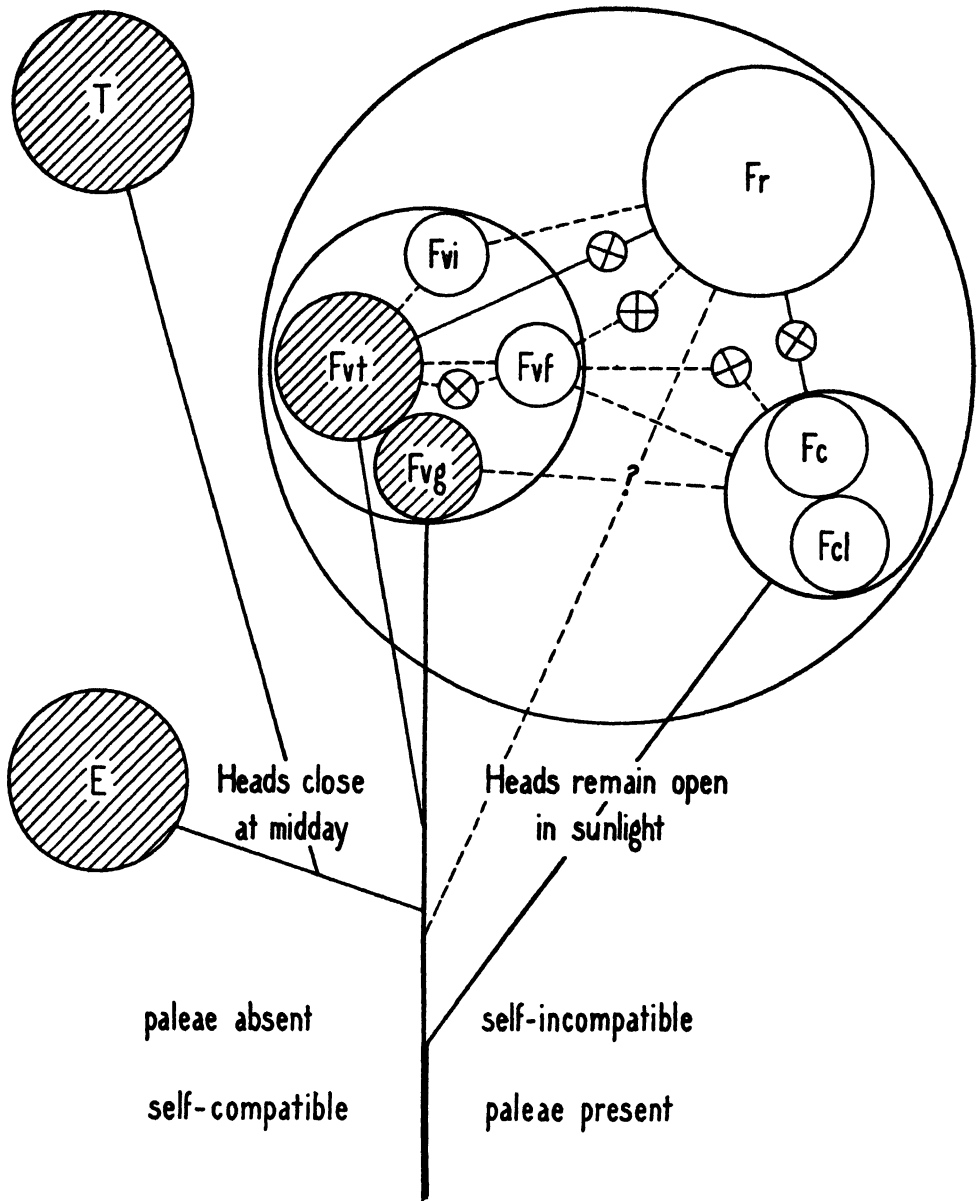


Fig. 222. Diagram representing the phylogenetic relations of *C. eritreensis* (E), *C. Thomsonii* (T), and *C. foetida* (F). Within *C. foetida* the 3 subspecies, *vulgaris* (Fv), *commutata* (Fc), and *rhoeadifolia* (Fr), are represented by the 3 larger circles. Within subsp. *vulgaris* the 4 variants, *typica* (Fvt), *glandulosa* (Fvg), *fallax* (Fvf), and *interrupta* (Fvi), are shown by smaller circles. Similarly, within subsp. *commutata* the 2 variants, Fc and Fcl, are shown. The very small circles enclosing crosses represent natural hybrids. Purely hypothetical connections are represented by dotted lines. Shaded circles indicate self-compatibility; unshaded circles, self-incompatibility.

148). Fourth, subsp. *rhoeadifolia* is known to be variable in its genetic factors for self-incompatibility. Fifth, some cultivated strains of typical subsp. *rhoeadifolia* have been observed to have low fertility. None of these separate facts alone may be significant, but altogether they lend considerable support to the hypothesis of the hybrid origin of this subspecies.

Several forms of *C. foetida vulgaris*, such as m.v. 13 and m.v. 48, may also have arisen through hybridization. They are actually intermediate in morphology, and m.v. 13 combines certain characters of subsp. *vulgaris* and subsp. *commutata*. Since they never have paleae, due to the presence of a dominant inhibiting gene, and since they show definite resemblance to subsp. *vulgaris* m.v. 1, they have been included under this subspecies.

The phylogenetic scheme shown in fig. 222 is much too simple to portray the amount of variation existing in *C. foetida*. In addition to the intergrading forms, some arising through hybridization and some through gene mutation, there are many environmental modifications which tend to make classification difficult. In other words, *C. foetida*, sen. lat., is essentially a Rassenkreis in which the three subspecies, in their more typical forms, are very distinct and easily recognized, but in which there are also many intermediate variants which must be classified more or less arbitrarily.

Although *C. eritreënsis* and *C. Thomsonii* are very closely related to *C. foetida*, as indicated by the fact that artificial hybrids between them and certain forms of *C. foetida* are highly fertile, yet they certainly differ in numerous genes, and both are so widely separated geographically from *C. foetida* that they never come in contact in nature (see also discussion of relationships under those two species).

Of the other species in this section, *C. Schimperii* is also very similar morphologically, but it has not been possible to investigate this species cytogenetically. It, too, is widely separated from *C. foetida* geographically. The same is true of the very little-known species, *C. tybakiensis* (q.v.). *C. Kotschyana*, on the other hand, even though it has 4 instead of 5 pairs of chromosomes, has been found by Sherman (see Part I, p. 21) to have certain segments in its chromosomes which are homologous with certain segments in the chromosomes of *C. foetida*, *C. Thomsonii*, and *C. eritreënsis*, also of *C. rubra*, *C. syriaca*, and *C. alpina*. This is very good evidence that at least 7 of the 9 species in this section originated from a common ancestral line. The same is probably true of the 2 species not yet investigated cytogenetically, *C. Schimperii* and *C. tybakiensis*.

146. *Crepis Schimperii* Sch. Bip.

Ex Schweinf., Fl. Aethiop., 144. 1867. (Fig. 223.)

Annual, (1) 1.5–3 dm high, the whole plant hispid with yellow setiform hairs; caudical leaves oblanceolate, acute or acuminate, dentate, pinnatifid or pinnately parted, lobes acute, sometimes dentate, attenuate into a narrowly winged petiole; lower cauline leaves similar, middle cauline leaves sessile, uppermost entire, linear, bractlike; stem erect, branched above or from near base, branches long, erect or occasionally spreading, mostly 1-furcate, bearing two heads; peduncles 1.5–10 cm long, often with one small bract about 1 cm below head, slightly thickened near base of head, densely setaceous or, like the involucre, sometimes shortly gland-pubescent and fuscous-tomentose and with a few setae; heads medium, nodding while young, erect in flower and fruit, about 60-flowered; involucre cylindric-turbinate, about 10 mm high, 8 mm wide; outer bracts 10, unequal, up to $\frac{1}{2}$ as long as inner ones, usually darker in color, linear, acuminate, like inner ones \pm setaceous with long yellow glandless hairs; inner bracts 15–20, equal, lanceolate, acute, becoming carinate and spongy-thickened dorsally, ventrally glabrous below and pubescent with yellowish hairs above; receptacle areolate-fimbriate, fimbriae low, membranous, ciliate with white hairs 0.25 mm long; corolla about 10 mm long; ligule about 0.8 mm wide; teeth 0.25 mm long, obtuse; corolla tube 5 mm long, very slender, glabrous below, sparsely beset above, as on base of ligule, with acicular hairs up to 0.5 mm long;



Fig. 223. *Crepis Schimperi*, a, c-f, from Schimper 929 (Bo); b, from Schimper 295 (Bo); g-k, from Schimper 65 (B): a, b, plants, $\times \frac{1}{2}$; c, fruiting head, $\times 2$; d-f, marginal and inner achenes and a pappus seta, $\times 8$; g, floriol lacking ovary, $\times 4$; g', detail of ligule tooth, $\times 50$; h, anther tube, $\times 8$; i, detail of appendages, $\times 32$; k, detail of receptacle, $\times 25$.

anther tube 1.8×0.75 mm dis.; appendages 0.6 mm long, acuminate; filaments 0.25 mm longer; style branches 1 mm long, 0.1 mm wide, obtuse, yellow; achenes 8–10 mm long, about 0.75 mm wide, uniform, the marginal shorter, curved, reddish-brown fading to yellowish-brown above, fusiform, slightly contracted at the calloused base, gradually attenuate into a rather coarse beak equal to body, about 15-ribbed, ribs fine, spiculate with acute scales about 0.25 mm long; pappus yellowish, 5–6 mm long, 2-seriate, fine, completely extruded at maturity, persistent. Flowering Aug.–Jan.; flowers yellow, ligule teeth reddish-purple.

Barkhausia Schimper Sch. Bip., ex A. Rich., Voy. Abyss. 1: 466. 1847.

Hieraciodes Schimper O. Kuntze, Gen. 1: 346. 1891.

Central and N. Abyssinia, 1600–2200 m, mountains and hills, fields and waste places; abundant around Abba Gerima in 1862.

Type collection, Schimper iter Abyss., sec. 1, no. 295: plantae Adoënsis. Plants are somewhat variable in size and habit as a result, no doubt, of variations in local environmental conditions. They are more robust under cultivation (cf. spec. in Herb. Hort. Berol.) but retain the distinctive features of leaves, habit, and inflorescence.

Monomorphic.

Abyssinia: near Adua, on hills, *Schimper 295* (K, B, Bo, P, PC, Fl, UCf); without definite locality, *Schimper 929* (K, Bo, P, PC, UCf); Abba Gerima, waste places, 2200 m, *Schimper 83* (B, UCf, US); Semen, Debra Eski, barley fields, 1600 m, *Schimper 65* (B, Stockholm, PC, UCf); Dschadscha, "auf Bergen," 1700 m, *Schimper* (B); Ataba, *Schimper* ? (B); Chiré, Konaleta, *Dillon 547* (P); without definite locality, *Dillon* in 1840 (DL).

Crepis Schimper is closely related to *C. eritreënsis*, but it is clearly distinguished from the latter by the hispid indumentum, especially on the involucre, by the furcate, 2-headed branches and longer peduncles, by the copious, longer, yellow pappus, by the reddish-brown achenes which are shorter, slightly wider, more coarsely beaked, with beak equal to body, by the shorter, narrower ligules and longer corolla tubes, by the style branches which are much shorter, by the anther tube appendages which are longer, acuminate, and by the caudical leaves which are narrowly petioled, whereas those of *C. eritreënsis* have broadly winged petioles. Furthermore, *C. Schimper* flowers during the autumn and winter, whereas *C. eritreënsis* is a spring flowering plant, this alone, however, not distinguishing them as species. Although they occupy rather closely adjacent areas, these two species are apparently confined to different altitudes, *C. Schimper* ranging from 1600 to 2200 m (not, as stated by some authors, to 2800 or 3000 m, this being based on a misinterpretation of the altitude for *Schimper 65*, which is 5300 ft., not 9300 ft.), whereas *C. eritreënsis* occurs between 800 and 1400 m. Extensive field study, however, might reveal an overlapping of their areas and the consequent occurrence of hybrid forms. Living plants of *C. Schimper* have not been available for the present study, but it is probable that its chromosomes closely resemble those of *C. eritreënsis*. These two species have as their nearest relatives *C. Thomsonii* and *C. foetida*.

147. *Crepis* (*Barkhausia*) *Kotschyana* Boiss.

Diag. Pl. Or. Nov. ser. 1, 7: 13. 1846; Fl. Orient. 3: 852. 1875. (Fig. 224.)

Annual, 0.6–3 dm high; root vertical, slender, merging into the slender caudex and stem; caudical leaves few and very small to numerous and up to 16 cm long and 2.5 cm wide, linear to lanceolate or oblanceolate, acute or obtuse, denticulate or sometimes remotely pinnately parted with narrow acute lateral segments, teeth or lobes corneous-mucronate, finely ciliate on margin, glabrous, tomentulose or canescent-tomentose, often pubescent with pale glandless or glandular hairs; cauline

leaves numerous, conspicuous, the lowest similar to the caudical ones, the others obovate, oblanceolate, lanceolate or linear, apiculate, sessile, subamplexicaul or auriculate-amplexicaul, denticulate or dentate, usually \pm tomentose, often pubescent with or without glands; stem erect, simple and 1-headed, or dichotomously 1-many-branched, branches divaricate, pedunculate or rebranched, leafy, 2-12-headed, canescent-tomentulose, often hairy, with or without glands; peduncles 2-7 cm long, erect or arcuate, slender at base, gradually thickened toward summit, tomentose, usually hairy or setulose, with or without glands; heads nodding in bud, erect in anthesis and in fruit, small to medium, 40-114-flowered; involucre campanulate, 11-13 mm long, 8-10 mm wide, canescent-tomentose, densely setulose with long yellow glandless setules, or shortly gland-pubescent, or both setulose and gland-hairy; outer bracts about 3-10, appressed, mostly very short, occasionally the longest $\frac{1}{2}$ as long as inner, linear; inner bracts 12-15, lanceolate, acuminate, the inner face glabrous below and appressed-pubescent near the apex, becoming navicular, incurved, laterally compressed, enclosing marginal achenes, yellow and spongy-thickened on the keel; receptacle convex, areolate, with fleshy naked ridges between the areoles; corolla (in a medium-sized plant) 8-9.5 mm long; ligule 4.5-5.5 mm wide, pubescent on lower half of outer face with rather coarse 2-celled trichomes 0.1-0.4 mm long and with a few similar long or short trichomes near the ligule teeth; teeth 0.15 mm long; corolla tube 3.5-4 mm long, very slender, shortly pubescent at summit; anther tube about 2.4×0.75 mm dis.; appendages 0.5 mm long, acuminate; filaments 0.25 mm longer; style branches 0.7-0.9 mm long, slender, yellow; achenes stramineous or yellowish, biform, the marginal ones not beaked, the inner beaked, or in reduced forms the marginal ones sometimes strongly attenuate or shortly beaked; marginal achenes 4.5-6 mm long, 0.8-1.2 mm wide, strongly compressed laterally, oblong, shortly attenuate or constricted at apex, with slightly expanded pappus disk, incurved, ventrally spongy-thickened and smooth or \pm spiculate, dorsally striate, muriculate or spiculate, with an oblique basal scar; inner achenes 7.5-12.5 mm long, fusiform, abruptly or gradually attenuate into a slender beak as long or twice as long as the body, 10-striate, strongly spiculate under lens, the beak sometimes quite smooth, with expanded pappus disk, constricted at the very narrow obliquely calloused base; pappus yellowish-white, 4-6 mm long, 2-seriate, outer setae finer, coarsest up to 65μ (5 cells) wide, rather stiff but pliable, persistent. Flowering March-June; flowers pale yellow, with or without purple on outer face of ligule in marginal florets and with or without purple ligule teeth. Chromosomes, $2n = 8$.

Crepis Bureniana Boiss., Fl. Orient. 3: 852. 1875.

Barkhausia glanduligera Winkl., Acta Hort. Petrop. 11(9): 325. 1890.

Hieraciodes Burenianum O. Kuntze, Gen. 1: 345. 1891.

C. glanduligera B. Fedtsch., Rastit. Turkest. 765. 1915.

C. assyriaca Bornm., in herb.

Syria, near Damascus and Palmyra, and eastward through Iraq, Persia, Transcaspiian Prov., Baluchistan, Afghanistan, Turkestan; acc. to Clarke (252), in Hazara, North-West Frontier Prov.; reported by Fedtschenko (203) from Pamiroalai, Serawschan, and Urmitan. Found mostly in lower altitudes and often in dry, sandy, or rocky places.

The type, as it happens, is an extremely reduced form, and, hence, concerning the size of the plant and its parts, is not typical of the species. It was thought by Boissier that the achenes in the type collection, and in the other specimens cited in the original description, were sufficiently different from those of *C. Bureniana* to warrant the recognition of two species. Careful study of the material in the earliest

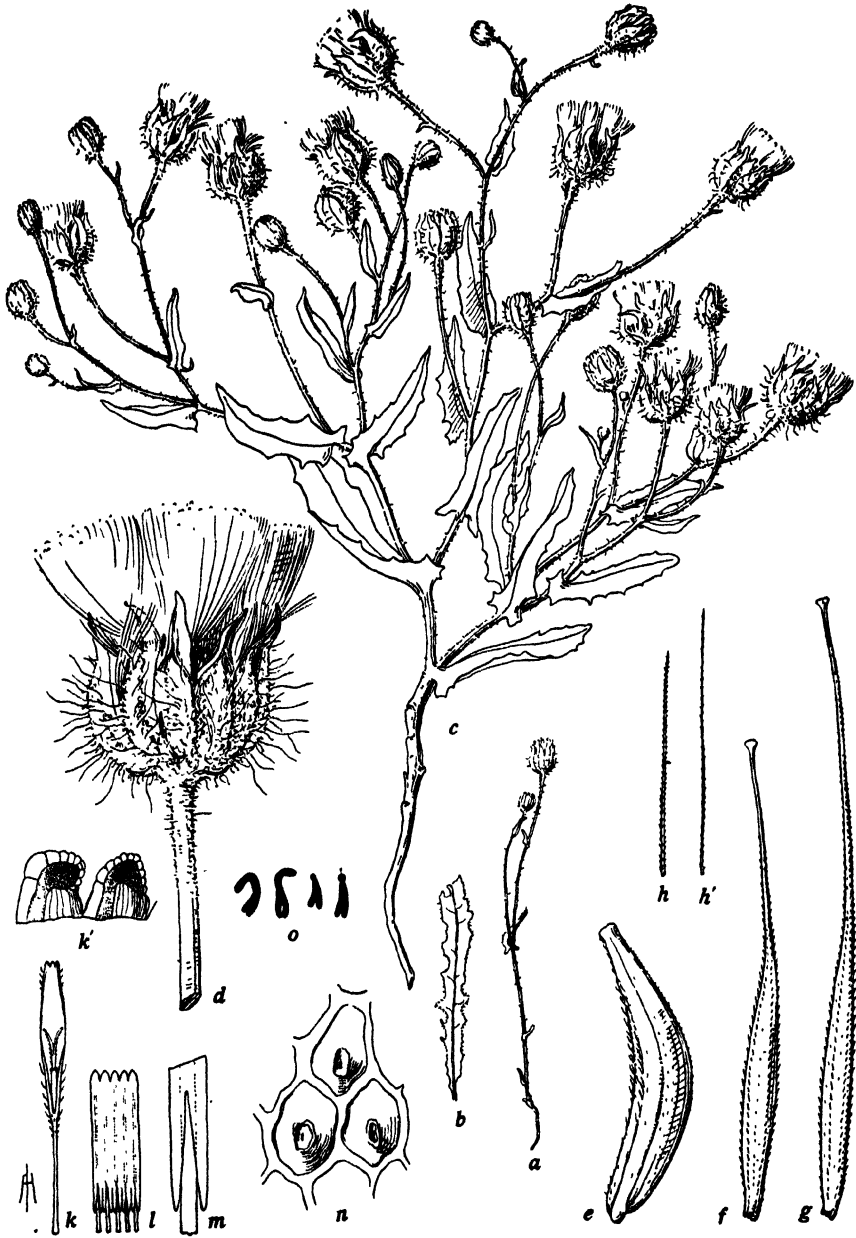


Fig. 224. *Crepis Kotschyana*, a, from isotype, Kotschy 173 (UC 313835); b, from Kotschy 289 (UC 313835); c-h', from Haussknecht in 1868 (Bo, as *C. Bureniana*); k-m, from Duthie in 1891 (K); n, from Stocks 1053 (Bo); o, from hort. genet. Calif. 1655 (grown from seeds received from E. Russian Turkestan through Dr. M. Navashin; cf. UC 633236): a, b, plant and leaf, $\times \frac{1}{2}$; c, plant, $\times \frac{1}{2}$; d, fruiting head, $\times 2$; e-h', achenes and pappus setae, $\times 8$; k, floret lacking ovary, $\times 4$; l, anther tube, $\times 8$; m, detail of appendages, $\times 32$; n, detail of receptacle, $\times 25$; o, somatic chromosomes, $n = 4$, $\times 1250$.

collections of *C. Kotschyana*, as represented in several herbaria, however, shows that even these delicate 1-2-headed plantlets, when sufficiently mature, sometimes, as in the type of *C. Bureniana*, have both marginal and inner achenes, although they are smaller. Furthermore, extremely reduced forms, like the type of *C. Kotschyana*, occur here and there in Persia and northward; they do not represent a geographic race. That they are probably caused by crowding and drouth is indicated by the fact that they occur along with more robust plants, such as would be considered typical of *C. Bureniana*, in the collection of Stocks from Baluchistan, cited below. The collection of Regel in 1883 from Turkestan, which was distributed to various herbaria as *Barkhausia glanduligera*, consists of plants which are intermediate in size between the type of *C. Kotschyana* and the type of *C. Bureniana*. Similarly with respect to the classic collection of Aucher-Eloy, no. 4876, from S.W. Persia, some of the plants were determined as *C. Kotschyana* and later some of them were identified as *C. Bureniana*. In other words, the combined evidence from all the critical specimens is consistent with the conclusion that the extremes in size, found in the types of *C. Kotschyana* and *C. Bureniana*, are connected by intergrading (and presumably interfertile) forms. At the same time, local races occur which are apparently distinct genetically, and these ecotypes further increase the polymorphism of this species (cf. m.v. 1 and 2).

Syria: around Damascus, Zohary in 1931 (UC) m.v. 2. **Iraq:** Kerkuk (Kirkuk), Haussknecht 616 (Bo) type of *C. Bureniana*; Erbil dist., Mt. Kuh-Sefin, Bornmüller 1501b (Weimar) as *C. assyriaca* ined.; *ibid.*, Bornmüller 1501, 1502 (Weimar) as *C. glandulosa* Presl. **Persia:** Kerman Prov., Sungur, Mt. Kuh-i-Emrullah, Strauss in 1908 (B) as *C. foetida* var. *glandulosa* Bornm.; *ibid.*, Kerind, Strauss in 1908 (Weimar); *ibid.*, Kerman, Mt. Kuh-tagh-ali, 2000 m, Bornmüller 5140 (B, P, PA) as *C. Bureniana* var. *glandulosa* Bornm. = m.v. 1; Kerman Prov., between Chabbis and Kerman, Bunge 283 (Bo) as *C. Bureniana*; Kerman Prov., Singar (Sinjar), in desert, Haussknecht in 1867 (P); Faristan Prov., Schapur, calcareous soil, among herbs, 850 m, Haussknecht in 1868 (Bo) as *C. Bureniana*; Faristan Prov., between Fasa and Schiraz, Aucher-Eloy 4876 (P) as *C. Bureniana*; *ibid.*; Aucher-Eloy 4876 (Bo) as *C. Kotschyana*; *ibid.*, Cheran, Aucher-Eloy 4876b (P) as *C. Bureniana*; Faristan Prov., Dalechi, among rocks, Kotschy 173, March, 1842 (Bo) type collection, type specimen is plant a, but these greatly reduced plants are not fully representative of the species; *ibid.*, Kotschy 173 (P, Fl, Mo) isotypes; *ibid.*, Persepolis, Kotschy 289 (Bo, P, Fl, Ms, Mo, UC); *ibid.*, Shiraz, Kotschy 69c (Bo); Gilan Prov., near Mendshil and Sturikherabad, Bornmüller 7530, 7522 (Weimar) as *C. glandulosa* Presl. **Transcaspien Province:** Karakala, just north of Persian border, ex hort. genet. Calif. 33.3226, cult. from seeds collected by M. Popov, June 13, 1931 (UC). **Turkestan:** Ourmitane Tchoukalik, Capus 811 (P) as *C. Bureniana*; Bucharra, Gasi-Mailik Mts., Regel in 1883 (P, B, BB, Fl) as *Barkhausia glanduligera* Winkl.; Fergan (Fergana, Ferghana), Mogol-Tau Mts., Fergan Valley, ex hort. genet. Calif. 31.1655, cult. from seeds received through M. Navashin (UC). **Baluchistan:** Stocks 827 (K) and Stocks 1153 (DD) as *C. Bureniana*; *ibid.*, Stocks 1053 and "in 1851" (Bo) as *C. Bureniana*, but some of these plants are much reduced and very slender, although no. 1053 is representative of the more robust forms of the species.

Minor Variants of *C. Kotschyana*

1. (*C. Bureniana* var. *glandulosa* Bornm., in herb.) Plants only 2-4 cm high, 2-5-headed; stem very short, branched from the base, the branches short, decumbent or nearly prostrate; heads nearly as large as in tall robust plants; leaves narrow. This unusual form is from the highest elevation known for the species. It is probably an ecotype, but should be tested with garden cultures, as has been done with m.v. 2. Bornmüller 5140 (B, P, PA), Mt. Kuh-tagh-ali, Kerman, Persia.

2. Plants 6-7 cm high, 7-headed; stem very short, branched from the base, the branches short, strict, or arcuate; heads fully as large as those in large robust plants; leaves narrow. Evidently an ecotype, although somewhat suppressed by the environment, since the cultivated progeny of this plant are 7-10 cm high and 4-9-headed. In the stiffly upright habit and divaricate branches this form is distinct from the preceding. Ex hort. genet. Calif. 32.3173 (UC), cult. from seeds taken from the following: Zohary in 1931 (UC), Damascus, Syria.

Relationship

Crepis Kotschyana, when compared morphologically with the other species in this section, is found to resemble them in many characters, especially in the achenes, which are more like those of *C. Thomsonii* and *C. foetida rhoeadifolia* than any of the other species. It is, however, very distinct from these species in habit, leaves, flowers, and fruits. *C. Kotschyana* is the only species in this section having 4 pairs of chromosomes, all the others having 5 pairs (except that the chromosomes of *C. Schimperii* and *C. tybakiensis* have not been seen). Because of this difference in chromosome number, it appears that *C. Kotschyana* acts as a natural barrier between *C. Thomsonii* on the east and *C. foetida* on the west, since any natural hybrids that might occur between *C. Kotschyana* and the other two species would certainly be less fertile than plants of either parent.

The cytogenetic relations between *C. Kotschyana* and its nearest relatives have been investigated by Mrs. Marta Sherman Walters (Part I, p. 21). In hybrids between *C. Kotschyana* and six other species of this section, she found that it was possible to identify the individual chromosomes of both parents during the diakinesis phase of meiosis. By analyzing many diakinesis configurations in each of the six hybrids, she was able to show that *C. Kotschyana* has in its 4 pairs of chromosomes some segments which are homologous (as indicated by pairing) with certain segments in the chromosomes of each of the six 5-paired species. This evidence supports the morphological evidence indicating that *C. Kotschyana* is genetically very close to *C. alpina*, *C. syriaca*, *C. rubra*, *C. foetida*, *C. eritreënsis*, and *C. Thomsonii*. In connection with her studies Sherman compared all seven species on the basis of twenty-five measurable characters and concluded that *C. Kotschyana* might be considered a more advanced species than the first four in the series mentioned above, but that in several characters it is less reduced than the last two in the series.

In view of this evidence it is inferred that the reduction from 5 to 4 pairs of chromosomes occurred in a common ancestor of the seven species mentioned above at a time when it was widely distributed in S.W. Asia, and that various 5-paired species became differentiated subsequently through the combined effects of gene mutations and environmental changes.

148. *Crepis eritreënsis* Babc.

Jour. Bot. 76: 208. 1938. (Fig. 225.)

Annual, 2.5–5.5 dm high, the whole plant hispidulous with fine soft yellow glandular and glandless hairs mixed; caudical leaves oblanceolate, obtuse or acute, irregularly denticulate or coarsely dentate, gradually attenuate into a broadly winged petiole; lowest cauline leaves similar or shortly petioled and pinnatifid with shallow triangular lobes; middle and upper cauline leaves sessile, lyrate-pinnatifid, the middle ones with close narrow lobes, \pm crumpled, the upper ones with more remote deep narrow lobes which are sometimes congested near the subauriculate base, uppermost leaves laciniate-subauriculate; stem simple, erect, sinuate below, branched above, branches long, strictly ascending, corymbosely 3-headed, or stem divaricately branched from base, branches long, arcuate or strictly ascending, leafy, \pm branched, ultimate branches corymbosely 2–3-headed, branchlets with young heads drooping; peduncles 1–5 cm long, naked or with 1 or 2 small bracts near head, slightly thickened near base of head; heads medium, erect in flower and fruit, about 60-flowered; involucre cylindric-turbinate, 7–10 mm high, 7 mm wide; outer bracts 11, unequal, longest scarcely $\frac{1}{2}$ as long as inner bracts, like inner bracts, green with deep purple ciliate tips, linear, acuminate, ultimately spreading; inner bracts 12

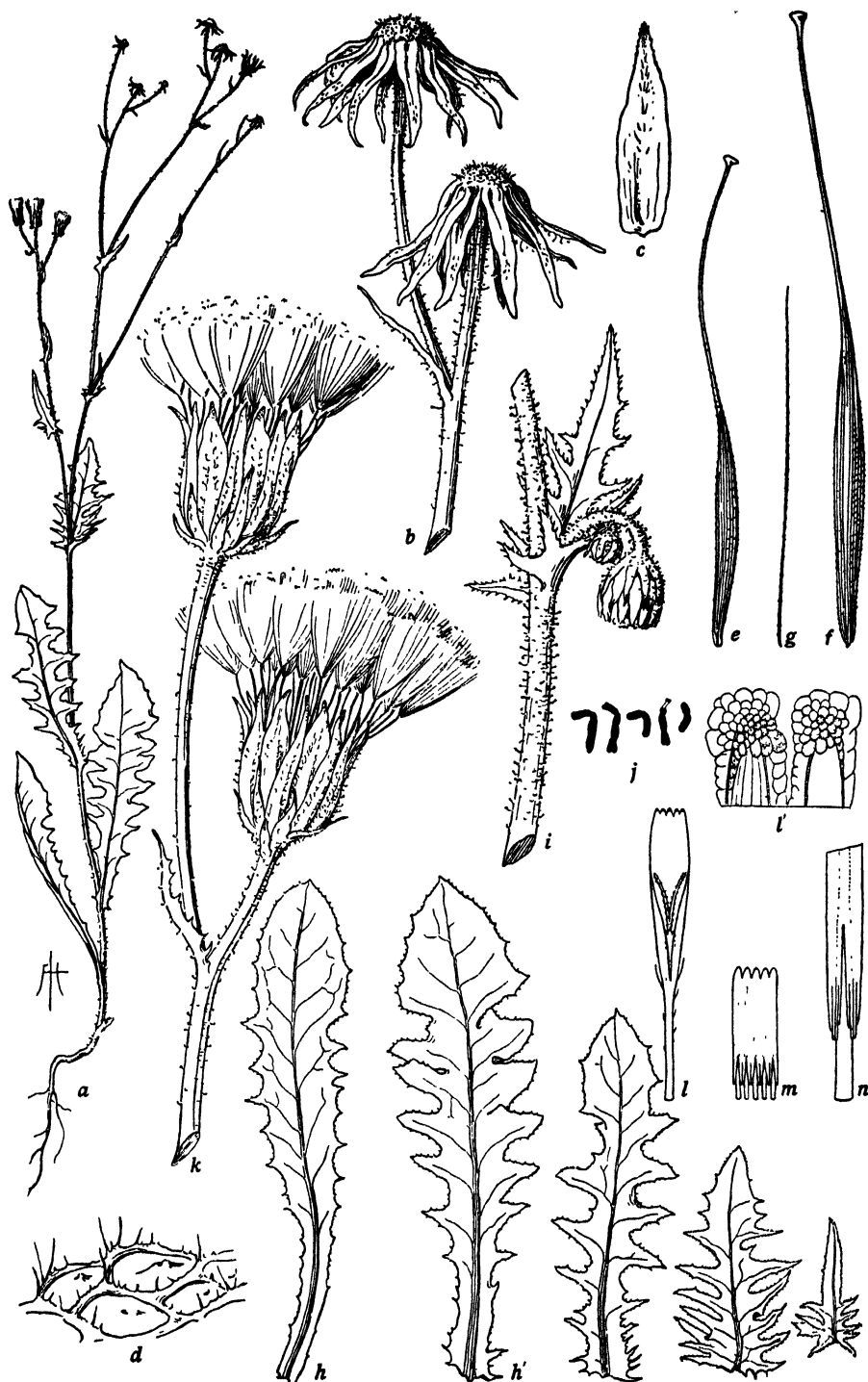


Fig. 225. *Crepis eritreensis*, a-g, from type (US 829670); h-n, from hort. genet. Calif. 32.3005 (UC 482447): a, plant, $\times \frac{1}{4}$; b, 2 old heads, $\times 2$; c, inner involucre bract, inner face, $\times 4$; d, detail of receptacle, $\times 25$; e-g, 2 achenes and a pappus seta, $\times 8$; h, h', 1 caudical and 4 cauline leaves, $\times 1$; j, part of inflorescence, $\times 2$; j, somatic chromosomes, $n=5$, $\times 1250$; k, 2 nearly mature heads, $\times 2$; l, floret lacking ovary, $\times 4$; l', detail of ligule teeth, $\times 50$; m, anther tube, $\times 8$; n, detail of appendages, $\times 32$.

or 13, equal, lanceolate, acute, becoming carinate and spongy-thickened dorsally, ventrally glabrous below, pubescent with yellowish hairs above; receptacle areolate-fimbriate, areolae 0.3–0.5 mm wide, fimbriae low, membranous, ciliate with white hairs 0.25 mm long; corolla 10 mm long; ligule up to 1.25 mm wide; teeth 0.25 mm long, obtuse; corolla tube 4 mm long, glabrous except a few hyaline acicular hairs up to 0.4 mm long; anther tube 2×0.75 mm dis.; appendages 0.5 mm long, acute; filaments 0.25 mm longer; style branches 1.75–2 mm long, 0.1 mm wide, obtuse, yellow; achenes uniform (but the marginal ones shorter), dark brown when mature, 8–11 mm long, body 3.5 mm long, 0.5 mm wide, rather abruptly attenuate into a very slender beak 2–3 times as long as body, funnel-shaped below the pappus disk, constricted at the narrow calloused base, 15-ribbed, ribs fine, densely and finely spiculate with broad spicules 0.25–0.5 mm long; pappus 4–5 mm long, yellowish-white, very fine, delicate, persistent, extruded completely above involucre at maturity. Flowering (Feb. †), April, May; flowers yellow, ligule teeth reddish-purple. Chromosomes, $2n = 10$.

E. Eritrea from 800 to 1400 m alt.; one of the collections (hort. genet. Calif. 3005) was reported from a "comparatively moist, rocky formation."

Monomorphic.

Type collection, *Schweinfurth et Riva 2031*. The above description is based on this and specimens cited below, together with plants grown from seeds collected by H. Compere near Embaralla, about 1300 m alt., April 15, 1930 (hort. genet. Calif. 3005). It should be noted that the type specimen is tall, with a simple stem branched above, whereas the cultivated plants are lower and divaricately branched from the base. These habitat differences, however, are only such as would be expected under radically different environmental conditions. The type evidently grew in competition with other herbs, whereas the cultivated plants grew in pots having ample room.

Eritrea: Mogod Valley, E. base of Mt. Bizen, near Asmara, *Schweinfurth et Riva 2031* (US type, UCf, K); Mogod Valley, upper part, *Schweinfurth et Riva 1596* (BB, UCf); Hamasen (Asmara) reg., Cecca Valley, Ghinda, *Fiori 1897* (Fl, UCf); (†) Hamasen (Asmara) reg., Embatealla (= Embaralla †), *Fiori 1898* (Fl); *ibid.*, near Embaralla, along railway, 1370 m, *Compere* in 1930 (seeds) spec. ex hort. genet. Calif. 3005 (UC).

Crepis eritreensis is closely related to *C. Schimperii* (q.v.) of not far distant regions in Abyssinia, but it is certainly distinct from the latter; also, it occurs at somewhat lower altitudes and it flowers in the spring, whereas *C. Schimperii* flowers in the autumn and early winter. Like their nearest relatives, *C. Thomsonii* and *C. foetida commutata*, these species, are precocious annuals.

149. *Crepis Thomsonii* Bab.

Jour. Bot. 76: 208–209. 1938. (Fig. 226.)

Annual, 0.5–3.5 dm high; caudex very short, attenuate into a woody taproot; caudical leaves rosulate, up to 17 cm long, 3 cm wide, sometimes very small in reduced forms, oblanceolate, acute or obtuse, runcinate-pinnatifid with triangular denticulate segments or pinnately parted or dentate, the terminal and lateral segments corneous-mucronate, attenuate into a short winged remotely denticulate petiole with broader base, sparsely hispid with short stout yellow glandless bristles on both sides and more densely along margin and on midrib beneath; lower cauline leaves similar; middle and upper cauline leaves lanceolate, acute or acuminate, dentate or entire, sessile, subamplexicaul, \pm lacinate near base; stems several or many from the enlarged caudex, nearly erect or half-prostrate in reduced forms, remotely cymosely few-branched, branches long, pedunculate or 2–4-headed, terete,

striate, not fistulose, like peduncles and involucre shortly gland-setulose throughout; peduncles 1–15 cm long, only slightly enlarged and bearing 1–3 small bracts near base of head; heads large, nodding before anthesis, many-flowered; involucre broadly campanulate, 9–11 mm long, 7–11 mm wide at maturity; outer bracts 10–12, unequal, the longest $\frac{1}{2}$ as long as inner bracts at maturity, linear-lanceolate, obtuse, \pm keeled, with narrow scarious margins, usually with a few setules, becoming lax at maturity; inner bracts 12–16, nearly oblong, strongly attenuate above, the narrow summit obtuse and finely lanate, ventrally pubescent with white hairs near tip, dorsally beset with numerous or few short yellow glandular setae, becoming prominently navicular, enclosing the marginal achenes at maturity and then indurate and yellowish, with broad scarious margins; receptacle alveolate-fimbrillate, ciliate, alveolae 0.5 mm wide, fimbrillae 0.2 mm high, fleshy-membranous, cilia 0.3–0.5 mm high, numerous, white; corolla 7–9.5 mm long; ligule 0.8 mm wide, intense purple at tip; teeth 0.1–0.3 mm long; corolla tube 3–4.5 mm long, very slender, pubescent on upper part, also on lower part of ligule half as high as summit of anther tube, with 2–3-celled trichomes; anther tube 2×0.4 mm dis.; appendages 0.5 mm long, acute, united; style branches 0.75–1.25 mm long, very slender, yellow; achenes dark brown below, paler above, of two distinct shapes; marginal achenes 5.5–7.5 mm long, about 1 mm in greatest width, strongly laterally compressed, attenuate upward into a coarse yellowish beak with slightly expanded pappus disk, abruptly narrowed to the yellow slightly calloused base, with oblique dorsal yellow scar, about 20-ribbed, ribs unequal, rounded, strongly spiculate especially on ventral side; inner achenes 7.5–12 mm long, 0.4–0.5 mm wide, fusiform, attenuate upward into a slender yellowish beak $1\frac{1}{2}$ –2 times as long as body and expanded conically near the broader (0.3 mm wide) pappus disk, narrowed above the calloused yellow base, 20-ribbed, ribs rounded, finely spiculate, every fourth rib a little stronger, making the body obscurely 4-angled, outermost of the inner achenes curved, dorsoventrally compressed, others straight, subterete; pappus 5–6 mm long, pale yellowish, 2 seriate, fine, rather stiff, persistent. Flowering Apr.–June; flowers yellow, ligule teeth purple. Chromosomes, $2n = 10$.

N. and N.W. India, especially submontane Punjab, and in Afghanistan and Baluchistan, 600–2400 m alt.

India: Naini Tal (formerly Kumaon), Lankhet (= Ranikhet ?), 1818–2400 m, May, 1845, *Thomson 1037* (K type, P, Mu, G) the type collection also contains m.v. 2; *ibid.*, 1666 m, *Strachey and Winterbottom* (K, G); *ibid.*, (elevation ?), *Strachey and Winterbottom* (K) m.v. 1; *ibid.*, 2000 m, *Edgeworth 221* (K) m.v. 2; Ranikhet, 1515–1818 m, *Rainrubh* in 1856 (DD) m.v. 2; Almorah, fields, 1515–2121 m, common, *Madden* (K); Gurhwal (= Garwahl ?), 1515 m, *Stewart 195* (K) m.v. 2; Punjab, Kulu-Lahaul, *Drummond 22954* (K, UC) m.v. 2; Punjab, Jammu, 1818 m, *Thomson* in 1848 (K) m.v. 2; Punjab, Rawalpindi, *Atchison* in April, 1871 (K); Punjab, Kangra, Baijnath, 900 m, *Koels 4506* (US) m.v. 2; Kangra, Bhadwar, 600 m, *Koels 4334* (US) m.v. 4; Kangra, Kulu, 1515 m, *Koels 4773* (US); Punjab, Hasan Abdal, 763 m, *Stewart 10938* (UC); N.W. Himalaya, Tarizha, *Martin 1854* (Calcutta) m.v. 3; North-West Frontier, Peshawar, 305 m, *Nath 15482* (UC) m.v. 4. **British Baluchistan:** Fort Sandeman, *Harsukh 20569* (K) m.v. 2; Baluchistan, *Stocks 1053* (K); *ibid.*, *Stocks 1153* (K, DD) m.v. 2. **Afghanistan:** *Griffith 945* (K) m.v. 2.

Minor Variants of *C. Thomsonii*

1. Low, with numerous rather large caudical leaves forming a dense matlike rosette and numerous short erect 1–2-forked stems. Perhaps this variant results from the combination of high altitude and abundant moisture. *Strachey and Winterbottom* (K), Naina Tal, N. India.

2. Low, with few rather small caudical leaves and few or many short half-prostrate 1–3-forked stems. Probably these variants result from combinations of drouth and sterile soil. The specimens cited below are all from India except the last three. *Thomson 1037* (K, P, Mu, G), in type collection, Lankhet (= Ranikhet ?), Naina Tal (formerly Kumaon); *Rainrubh* in 1856 (DD), 1515–1818 m, Ranikhet; *Edgeworth 221* (K), Naini Tal; *Stewart 195* (K) Garhwal (Gurhwal); *Drummond 22954* (K, UC), Punjab, Kulu-Lahaul; *Thomson* in 1848 (K), Punjab, Jammu;



Fig. 226. *Crepis Thomsonii*, a-o, from Thomson 1037 (K); p, from hort. genet. Calif. 3208 (grown from seeds received from Dr. R. R. Stewart; cf. UC 506850, 602780, 602781): a, plant, $\times \frac{1}{2}$; b, apical part of a leaf, $\times 2$; c, flowering head, $\times 2$; d, fruiting head, $\times 2$; e, detail of receptacle, $\times 25$; f, floret lacking ovary, $\times 4$; f', detail of ligule teeth, $\times 25$; g, anther tube, $\times 8$; h, detail of appendages, $\times 32$; k, mature inner involucre bract enclosing achene, $\times 8$; l-o, 3 achenes and a pappus seta, $\times 8$; l', n', barbs on achenes, $\times 50$; p, somatic chromosomes, $n = 5$, $\times 1250$.

Harsukh 20569 (K), Fort Sandeman, British Baluchistan; *Stooks 1153* (K), Baluchistan; *Griffith 945* (K), Afghanistan.

3. Low, with few large caudical leaves and about 4 short erect or ascending 1-4-headed stems. Probably the result of sudden drouth. *Martin 1854* (Calcutta), Tarizha, N.W. Himalaya.

4. Extremely reduced; plant 2.5-7 cm high, with few small leaves and a very slender 1-2-headed stem; flowers correspondingly reduced. *Koels 4334* (US), 600 m, Bhadwar, Kangra, Punjab.

Relationship

Although *Crepis Thomsonii* has long been confused with *Crepis foetida vulgaris*, it is very distinct from that species in the much smaller corolla and anther tube and in shape of the achenes. Certain morphological resemblances and differences

TABLE 18

COMPARISON OF SPECIMENS OF CREPIS THOMSONII IN HERB. KEW

(All measurements are in millimeters and represent averages of two or more heads)

Number	Bracts			Corolla	Involucral setae		Region
	Outer	Inner	I:O*		Coarseness	Glands†	
25A..	6	10 8	1.79	...	medium	+	Kumaon
25B..	4 8	10	2 11	...	medium	+	British India
26..	5 3	10	1.90	8 2	fine, medium	±	Kumaon
27A..	4	8.8	2 18	7.3	medium	+	British India
27B..	5	10 8	2 05	9.5	medium	+	British India
28..	4 5	10	2.22	8.0	medium	+	Kumaon
29A-C..	4 3	9 3	2.18	8 5	{coarse medium	{- +}	British India
30C..	5	9 8	1 95		medium	+	British India
31..	4 8	9.8	2 05	9 3	very fine	+	Kumaon
32..	5 3	11	2.10	..	medium	+	British India
33..	5 3	10 5	2 01	7.0	medium	+	Punjab
34A..	5 3	10	1 90	7 5	coarse	+	Baluchistan
35A..	5	12	2 41	8 0	medium	+	Baluchistan
35B..	5	11	2 20	7 5	medium	+	Afghanistan
40..	5 5	10 3	1 86	8 2	medium	±	Baluchistan
Averages ..	5	10 3	2 06	8 1			

* I:O = length of inner divided by length of longest outer bracts.

† Glands present indicated by +; absent, by -.

between *C. Thomsonii* and *C. foetida* are clearly shown by comparing the statistical data in table 18 with those in table 17. It will be seen that the ratio of length of outer to inner involucre bracts is almost identical with that of *C. foetida vulgaris*, and that the pubescence of the involucre is more like that of subsp. *vulgaris* than of subsp. *rhoeadifolia*, but that in length of corolla, *C. Thomsonii* averages much lower than any known forms of *C. foetida*. The marginal achenes in *C. Thomsonii* are more strongly compressed laterally and correspondingly wider dorsoventrally, whereas the inner achenes are lightly but definitely 4-angled. Also, the inner involucre bracts in *C. Thomsonii* are more strongly navicular, which causes the mature heads to be more conspicuously swollen at the base than in *C. foetida*. Along with these characters, *C. Thomsonii* always has several or many stems (except in m.v. 4), whereas this habit appears in only certain variants of *C. foetida*. Finally, no subspecies of *C. foetida* is known to occur farther east than the Caspian reg., whereas *C. Thomsonii* is not known west of Afghanistan. In the intervening area is found *C. Kotschyana* (with 8 chromosomes), to which *C. Thomsonii* shows certain affinity. *C. Thomsonii* also has many features in common with *C. eritreënsis* (q.v.). But, as shown by Sherman, there is good cytogenetic evidence that many structural differences exist in the chromosomes of these two species.

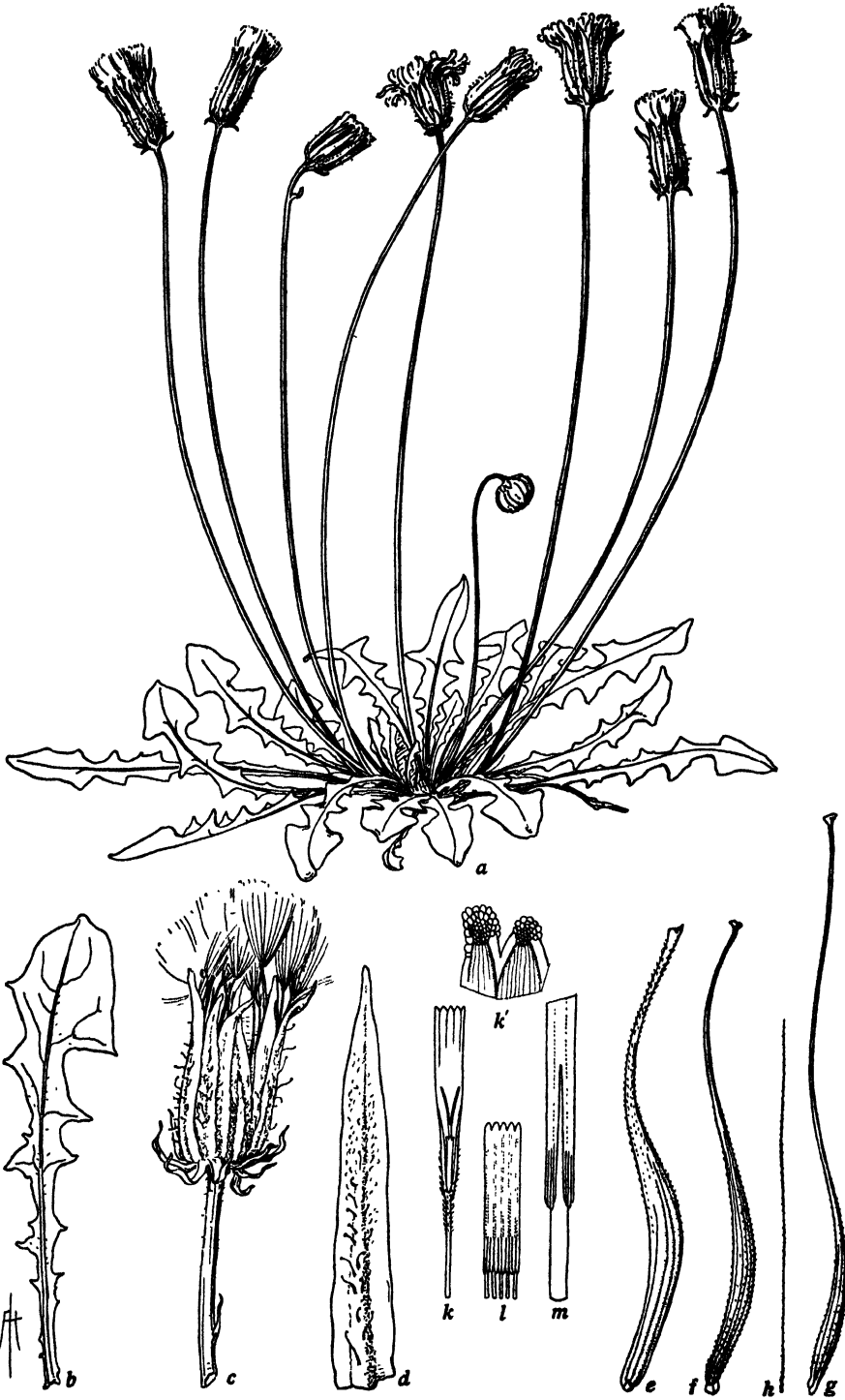


Fig. 227. *Crepis tybakiensis*, from type (UWG): a, plant, lacking root, $\times \frac{1}{2}$; b, leaf, $\times 2$; c, fruiting head, $\times 2$; d, inner involucre bract, outer face, $\times 4$; e-h, 3 achenes and a pappus seta, $\times 8$; i, floret lacking ovary, $\times 4$; j, detail of ligule teeth, $\times 32$; k, anther tube, $\times 8$; l, detail of appendages, $\times 32$.

150. *Crepis tybakiensis* Vierh.

Oesterr. Bot. Zeitsch. 65: 73. 1915. (Fig. 227.)

Annual (or perennial ?), about 1.5 dm high; leaves all basal, numerous, forming a small dense rosette, glabrous, subcarnose, up to 7 cm long and 1 cm wide, oblanceolate-linear, gradually attenuate into the narrowly winged petiole, pinnately parted, lateral lobes 3–5, mostly opposite, triangular, acute, remotely denticulate, terminal lobe ovate-hastate, obtuse-mucronate, acute or acuminate, remotely denticulate; scapes several, arcuately erect, 1-headed, slender, not fistulose, when young minutely gland-pubescent and sparsely canescent-tomentose near head, becoming glabrescent or glabrous, with 1–2 small linear bracts; heads medium, nodding while young, erect in flower and fruit, about 75-flowered; involucre cylindric-campanulate, about 12 mm high, 7–8 mm wide at maturity; outer bracts 10–15, unequal, longest up to $\frac{1}{3}$ as long as inner ones, linear, glabrescent; inner bracts 12–14, lanceolate, obtuse, thinly membranous, purplish-green, glabrous within, ultimately narrowly keeled dorsally, keel pale brown, enclosing marginal achene, minutely gland-pubescent with very fine short pale hairs and ellipsoidal brown glands, canescent-tomentulose; receptacle plane, areolate-fimbriate, fimbriae membranous, sparsely ciliate with very fine white hairs up to 0.25 mm long; corollas 8.5–10.5 mm long; ligule 1 mm wide, teeth 0.2 mm long; corolla tube 3.5 mm long, slender, puberulous with white acicular hairs up to 0.25 mm long; anther tube 2.25×0.65 mm dis.; appendages 0.6 mm long, narrow, oblong-acute; filaments 0.4 mm longer, very slender; style branches about 1.5 mm long, 0.05 mm wide, yellow; achenes nearly black when mature, with paler beak, bifurciform; marginal ones mostly 6–8 mm long, strongly curved, body equal to beak, ventrally plane, dorsally convex with conspicuous scar near the pale-calloused base, obscurely ribbed, ribs densely spiculate, beak coarse, about 0.2 mm wide, slightly expanded at the apex; inner achenes 10–12 mm long, beak about 2.5 times as long as body, extremely fine, 0.05 mm wide, abruptly expanded at summit to 0.25 mm wide, minutely spiculate or glabrous, body curved-fusiform, gradually attenuate at both ends, subterete, 10-ribbed, ribs rounded, spiculate, somewhat thickened at the constricted yellow-calloused base; pappus 5–6 mm long, pale-tawny, rather copious, 2–3-seriate, persistent, coming away singly. Flowering April; flowers yellow, ligules reddish-purple on outer face.

Known only from the type collection, consisting of 2 plants.

Monomorphic.

Crete: S. coast, Tybaki, Nábělek in 1914 (UWG, UCf).

Vierhapper (*loc. cit.*) has called attention to the general similarity of this plant to *Crepis radicata* Smith non Forskål, but his comparison is based only on the descriptions and illustration of the latter species (cf. Sibthorp et Smith, *Flor. Graec. Prod.*, 2: 136. 1813; *Flora Graeca*, 8: 74. tab. 800. 1833). Specimens of Halacsy, Orphanides, and others, which were identified as *C. radicata* Smith, upon examination have proved to be variants of *C. foetida vulgaris* (cf. m.v. 14, p. 692). Similarly, specimens of *C. foetida* var. *maritima* Boiss. and of *Barkhausia triangularis* C. Koch have also turned out to be variants of *C. foetida vulgaris* (cf. m.v. 14, p. 692 and m.v. 12, p. 692).

Relationship

Crepis tybakiensis shows definite resemblance to *C. rubra* in the scapiform stems and glabrescent outer involucre bracts. It is also similar to *C. rubra* in leaf shape. Although it is a much more reduced plant than *C. rubra*, especially in size of florets and achenes, it seems very probable that the two species had a common ancestor.

This marked tendency to reduction in size is found in most of the *Crepis* species endemic in Crete (cf. *C. cretica*, *C. Mungierii*, *C. Raulini*, and *C. Sibthorpiana*). On the basis of its rather narrow involucre, small florets, and slender, very finely beaked achenes, *C. tybakiensis* is the most advanced species in this section.

Addendum.—*C. tybakiensis* is certainly distinct from *Crepis flexiscapa* Rech. f. (Denkschr. Ak. Wiss., Wien, Math.-Naturwiss. Kl. 105[2] : 164. 1943), the publication of which was brought to my attention too late to permit the disposition of this interesting new species in its proper place in this monograph. No specimen of this species has yet been seen by me, but the original description and illustration suggest that it may belong in section 26.

SECTION 21. MICROCEPHALUM

This small group of species is definitely related to the most primitive species in the genus, since the four species comprising it are rhizomatous and the habit of the plant indicates a connection with secs. 1-5. But in each of these four species the reduction in size of the involucre, florets, and achenes is comparable to that of the most advanced species in the genus. Also, the inner involucre bracts become

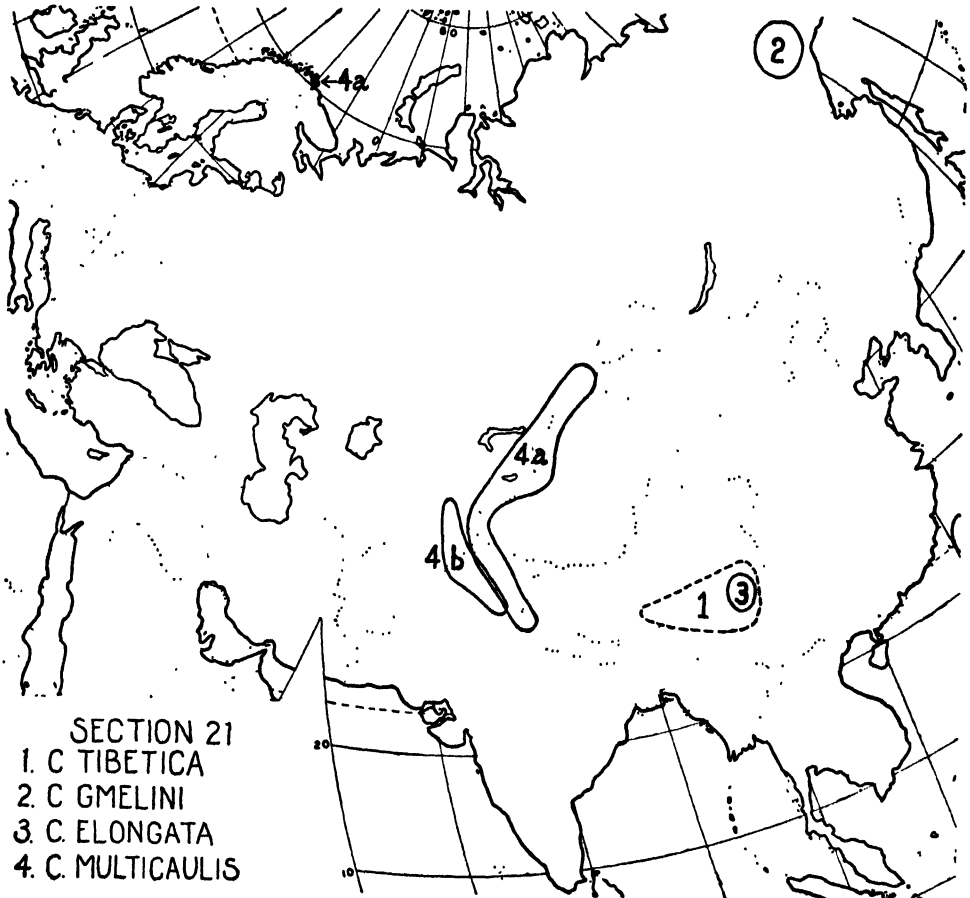


Fig. 228. Geographic distribution of the 4 species in sec. 21. Based on Goode *Base Map No. 201 PC*.
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more or less carinate and thickened in fruiting heads. For these reasons this section has been placed among the more advanced sections of the genus. In *C. tibetica*, *C. Gmelini*, and *C. elongata* the rhizome is elongated and horizontal or oblique and the stem is tall and paniculately branched, whereas in *C. multicaulis* the rhizome is prae-morse and the stem shorter and shortly branched at the top. The first three species, therefore, are more primitive. Furthermore, they are all monotypic endemics of restricted distribution. But *C. multicaulis* is a polymorphic widespread species. Hence the distribution of the four species is especially interesting (cf. fig. 228). *C. tibetica* is distributed in S.E. Tibet and S.W. China. *C. elongata* is restricted to a much smaller area in S.W. China. And *C. Gmelini* is known only from the Okhotsk reg. in N.E. Siberia. In marked contrast is the distribution of *C. multicaulis*, in which

subsp. *genuina* ranges from the Altai reg. southwestward through the Tien Shan and Ferghana regions to Kashmir and then southeastward in the W. Himalaya Mts. to Nepal; and subsp. *congesta* occurs in a similar narrow belt running from Lahul in the Punjab to Hazara in the North-West Frontier Prov. and northward to the Alai Mts. in Turkestan. Furthermore, it is especially noteworthy that *C. multicaulis genuina* also exists today in Varanger, a small area in the extreme north of Norway, just above the 70th parallel; and, according to Hulten's map of maximum Pleistocene glaciation (Hulten, pl. 44), Varanger is closely adjacent to an unglaciated area in N. Norway. Thus, it may be assumed either that Varanger was also unglaciated or that this plant has spread from an unglaciated district to its present location since the Ice Age. Thus, we find in sec. *Microcephalum* 3 rather primitive species, 2 endemic in S.E. Asia and 1 in N.E. Asia, whereas the more advanced member of the group has a wide distribution running southward from N. Central Asia and exists also on a small area in the extreme north of Norway. The whole picture is consistent with the hypothesis that the genus as a whole had its origin and early development in N. Central Asia in pre-Pleistocene time and that migrations radiated in all directions from that center. The great gap in the present distribution of *C. multicaulis genuina*, between Central Asia and N. Norway, necessitates the assumption that this species was continuously distributed in N. Europe and W. Siberia before the Ice Age. The 3 endemic species may also be assumed to have been of much wider distribution in pre-Pleistocene times.

Key to the Species of Section 21

Outer involucre bracts 6–10, the longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner; florets 9–14 mm long.

Caudical leaves with the petiole $\frac{1}{3}$ – $\frac{1}{2}$ as long as the blade; inner involucre bracts 12–14; corolla 9–10 mm long; anther tube 2–2.5 mm long; style branches dark green..... 151. *C. tibetica*, p. 721

Caudical leaves with the petiole longer than the blade; inner involucre bracts 10–12; corolla about 14 mm long; anther tube 4 mm long; style branches yellow..... 152. *C. Gmelini*, p. 723

Outer involucre bracts 5–7, the longest $\frac{1}{6}$ – $\frac{1}{4}$ as long as the inner; florets 6–8 mm long.

Plants mostly taller, 3–6.5 dm high; stems stouter; involucre in fruiting heads 9–10 mm long, 3–5 mm wide; ligules 5-toothed; filaments shorter than the anther tube; style branches black or dark green; achenes 0.6 mm wide..... 153. *C. elongata*, p. 725

Plants mostly shorter, 1–4 dm high; stems more slender; involucre 7–9 mm long, 2.5–3 mm wide; ligules often 4-toothed; filaments longer than the anther tube; style branches yellow; achenes 0.3 mm wide..... 154. *C. multicaulis*, p. 726

151. *Crepis tibetica* Bab.

Univ. Calif. Publ. Bot. 14: 330. 1928. (Fig. 229.)

Perennial, 2.4–5.5 dm high, with horizontal or oblique rhizome sometimes branched with several caudices and with strong fibrous roots; caudical leaves few, persisting, up to 22 cm long, 2.2 cm wide, semierect, oblanceolate or lanceolate, acute or obtuse, dentate or runcinate-pinnatifid, the teeth or segments papillose-mucronate, tapering into a narrowly winged petiole $\frac{1}{3}$ – $\frac{1}{2}$ as long as the blade with broad clasping base, finely pubescent on both sides with short appressed glandless yellowish setiform hairs, becoming glabrate, with rather prominent pale midrib; cauline leaves few, bractlike, or lower ones similar to caudical leaves but short-petioled; stems 1–3 to a caudex, erect, rather stout, glabrous, striate, simple or 2–5-branched; branches remote, long, strictly erect, 2–6-headed, cymose-corymbiform; peduncles 0.5–4.5 cm long, not thickened near head, usually with 1 or 2 small bracts often near head, fuscous-tomentose, like involucre densely pubescent with long and

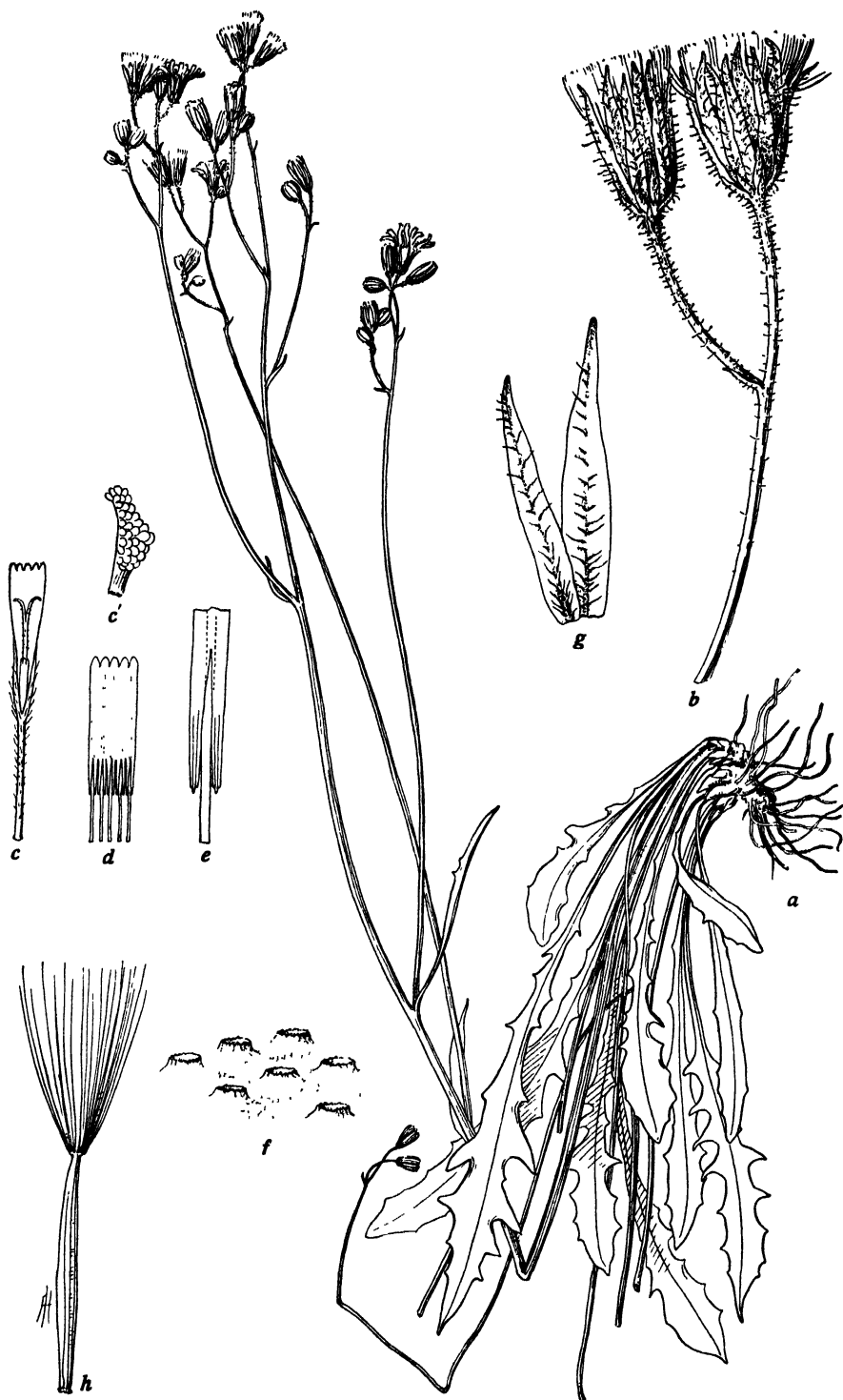


Fig. 229. *Crepis tibetica*, a-h, from type (K): a, plant, $\times \frac{1}{2}$; b, 2 immature heads, $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule tooth, $\times 50$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, detail of receptacle, $\times 25$; g, 2 inner involucral bracts, dorsal face, $\times 4$; h, achene and pappus, $\times 8$.

short glandular hairs, hairs mottled dark and pale green; heads erect, with about 30 florets; involucre before anthesis cylindric, 8–11 mm high, 2.5–3 mm wide at receptacle; outer bracts 7–10, unequal, longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner, lanceolate, acute; inner bracts 12–14, lanceolate, acute, scarious-margined, ventrally glabrous, dorsally with a darker median rib, obscurely spongy-thickened near base approaching maturity; receptacle punctate, glabrous; corolla 9–10 mm long; ligule 1.2 mm wide; teeth 0.2 mm long; corolla tube 4–4.5 mm long, densely pubescent with several-celled acicular hairs; anther tube yellow, 2.4×0.8 mm dis.; appendages 0.6 mm long, acuminate; filaments 0.8 mm longer; style branches dark green, 0.8 mm long, slender; achenes golden brown, 4–5 mm long, narrowly fusiform, subcompressed, strongly attenuate toward the narrow (about 0.2 mm wide) summit below the expanded (0.3 mm wide) paler pappus disk, constricted just above the narrow hollow base, about 10-ribbed, ribs nearly equal, very finely rugulose; pappus white, 4 mm long, 1-seriate, very fine, persistent. Flowering July–Aug., flowers yellow.

S. Tibet, W. Szechwan and Yunnan, 2700–3700 m alt. Type locality, W. Szechwan and Tibetan frontier, “chiefly near Tatsienlu.”

Tibet: Principality of Kiala, Tatsienlu, *Soulie* 750 (K); near Lhasa, Kyi Chu Valley, *Walton* in 1904 (K). **Szechwan:** chiefly near Tatsienlu, *Pratt* 599 (K, UCf) type. **Yunnan:** Tali Range, W. flank, lat. $25^{\circ} 40' N.$, 3000 m, *Forrest* 15608 (K, B) m.v. 1; S.E. Chungtien, near Hsia-Chungtien, 3700 m, *Feng* 1892 (G) m.v. 1.

Minor Variant of C. tibetica

1. Stems scapiform with a few short branches at the top forming a few-headed corymbiform cyme; style branches broader; achenes somewhat broader. *Forrest* 15608 (K, B) lat. $25^{\circ} 40' N.$, 3000 m, W. flank of Tali Range, Yunnan; *Feng* 1892 (G) near Hsia-Chungtien, 3700 m, S.E. Chungtien, N.W. Yunnan.

Relationship

Crepis tibetica is closest to *C. Gmelini*, with *C. multicaulis* and *C. elongata* next in order. Its habit resembles the larger forms of *C. multicaulis*, and the congested appearance of the young flower heads resembles a distinctive feature of *C. multicaulis congesta*. But in size of florets, anther tubes, and appendages, *C. tibetica* approaches more nearly to *C. Gmelini*, and no tendency to reduction in number of corolla teeth has been observed in the specimens available. It is distinct from *C. Gmelini* in the strongly attenuate achenes, much shorter and finer pappus, smaller florets, anther tubes, and appendages; and the whole plant is larger, the leaves are of different shape, pubescence, etc. It is less close to *C. elongata*, from which it differs notably in its corymbiform inflorescence, larger heads, longer outer involucre bracts, larger corolla, and narrower golden brown achenes.

152. *Crepis Gmelini* (L.) Tausch

Flora, 11(Erg.): 78. 1828. (Pl. 19. Fig. 230.)

Perennial, 1.5–3 dm high, with slender vertical praemorse rhizome bearing slender fibers; caudal leaves few, persisting, up to 7 cm long, 1.2 cm wide, semierect, oblanceolate or elliptic, acute or obtuse, sinuate-dentate, narrowed abruptly into a very slender winged petiole longer than the blade and with clasping base, sparsely and finely gland-pubescent on both sides with short white hairs, becoming glabrate; cauline leaves 3–4, linear, bractlike; stems 1 to a caudex, erect, slender, glabrous, finely striate, simple or cymosely few-branched above, branches 1–2-headed, somewhat spreading or arcuate; penduncles 2–4 cm long, thickened near head, 1–2-bracteate, canescent-tomentose and, like the involucre, with long and short mottled gland hairs; heads erect, with about 20 florets; involucre cylindrical, 9–11 mm high, 2.5–3 mm wide at base; outer bracts 6–10, unequal, longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as the

inner, lanceolate, acute; inner bracts 10–12, lanceolate, acute, scarious-margined, ventrally glabrous and prominently veined, dorsally dark in mid-region and becoming somewhat thickened; corolla about 14 mm long; ligule 1.2 mm wide, the 5 teeth 0.4 mm long; corolla tube about 5 mm long, densely pubescent with several-celled acicular hairs; anther tube yellow, about 4×1 mm dis.; appendages 0.8 mm long, acuminate; filaments 1.4 mm longer; style branches yellow, 1 mm long; achenes

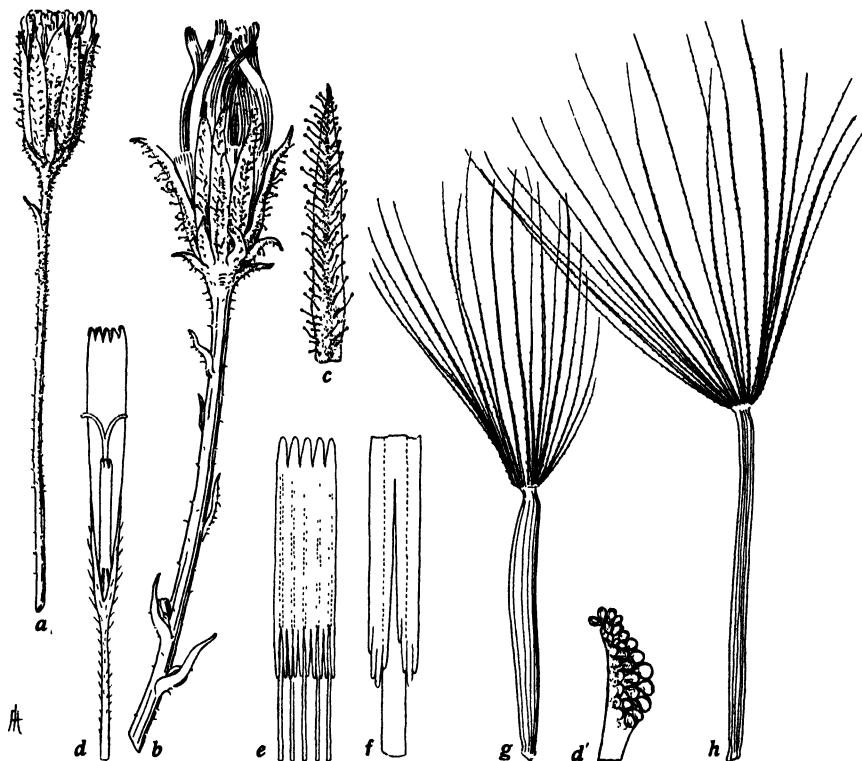


Fig. 230. *Crepis Gmelini*, a–f, from Turczaninow (acc. to Ledeb., Fl. Ros. 2: 824) in 1835 (K); g, from type (L); h, from authentic spec. of Tausch (PD): a, young head, $\times 2$; b, head after anthesis, $\times 2$; c, inner involucrel bract, outer face, $\times 4$; d, floret lacking ovary, $\times 4$; d', detail of ligule tooth, $\times 50$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, h, immature achenes with pappus, $\times 8$.

(immature) 4–5 mm long, fusiform, narrowed below the expanded pappus disk and near the calloused base, about 12-ribbed, ribs narrow, very finely rugulose; pappus white, 5–6 mm long, 1-seriate, fine, persistent. Flowers yellow.

Hieracium Gmelini L., Sp. Pl., ed. 1, 2: 802. 1753.

Crepis Gmelini Froel., ex DC., Prod. 7: 164. 1838.

C. multicaulis var. *ochotensis* DC., Prod. 7: 165. 1838.

C. multicaulis var. *macrocephala* Rgl., ex Regel, Rach and Herder, Bull. Soc. Nat. Moscou, 32: 217. 1859.

Hieraciodes Gmelini O. Kuntze, Gen. 1: 346. 1891.

E. Siberia, in the reg. of S.E. Yakutsk between the city of Yakutsk and the shore of the Sea of Okhotsk and between Okhotsk and Ayan. The long-existing confusion of this species with *C. multicaulis* Ledeb. makes the earlier reports of *C. Gmelini* from stations farther west very questionable (cf. Herder, 196).

Monomorphic.

Siberia: type (L, UCf); E. Siberia, *Tausch* (PD, UCf); *ibid.*, between Aldansk and Okhotsk, *Turczaninow* in 1835 (DC, UCf); between the Allach-Yuna R. and Okhotsk, *Turczaninow* † in 1835 (K, UCf).

Relationship

Near to *C. multicaulis* and, because of the superficial resemblance to the larger forms of *C. multicaulis typica*, often confused with that species; but more closely related to *C. tibetica* and *C. elongata*. The four species comprise a natural group. They exhibit some resemblance to *Crepis sancta*, especially subsp. *bifida* (cf. p. 756).

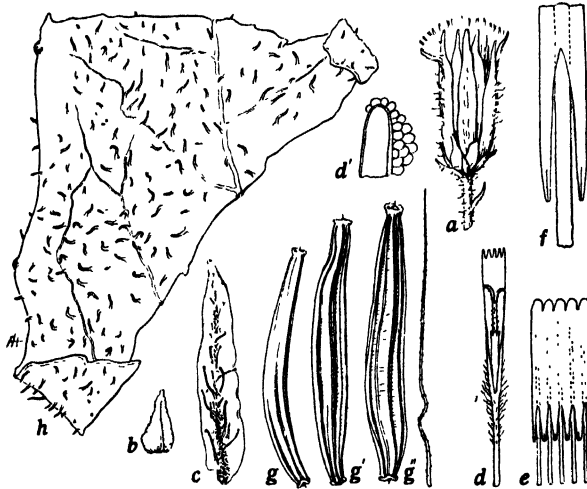


Fig. 231. *Crepis elongata*, from type (UWM): a, head, $\times 2$; b, c, outer and inner involucral bracts, outer face, $\times 4$; d, floret lacking ovary, $\times 4$; d', detail of ligule tooth, $\times 25$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, g', g'', outermost, intermediate, and innermost achenes and pappus seta, $\times 8$; h, fragment of leaf, showing pappilose setae, $\times 4$. Cf. pl. 20.

153. *Crepis elongata* Babc.

Univ. Calif. Publ. Bot. 14: 326. 1928. (Pl. 20. Fig. 231.)

Perennial, 3–6.5 dm high, with a long (?) oblique rhizome and many fibrous roots; caudical leaves up to 13 cm long, 1.5 cm wide, numerous, erect, oblanceolate, acute or obtuse, runcinate-pinnatifid or dentate, tapering into a winged petiole, hispidulous with short yellowish glandless hairs; lowest cauline leaves similar to caudical ones, all others much reduced, linear, entire; stems several or only 1 (9 in type), erect, elongated, 1–2-branched above, hispidulous near base, striate and glabrous above rosette; branches long, fastigiate, cymosely 2–4-headed; peduncles 0.5–3 cm long, slender, like involucre canescent-tomentose and densely pubescent with unequal mottled gland hairs; heads erect, small, 30-flowered; involucre cylindric in anthesis, campanulate in fruit, 9–10 mm high, 3–5 mm wide; outer bracts 5–6, unequal, longest $\frac{1}{4}$ as long as inner ones, lanceolate, acute; inner bracts 12, lanceolate, acute, innermost ones with membranous margins, becoming spongy-thickened dorsally near base, ventrally glabrous and nerved; receptacle naked; corolla 7.5–8 mm long; ligule 0.75 mm wide; teeth 0.3 mm long, obtuse; corolla tube 3 mm long, slender, densely white-pubescent with several-celled crinkled hairs; anther tube yellow, about 2×1 mm dis.; appendages 0.6 mm long, acuminate; filaments 0.6 mm longer; style branches 0.6 mm long, 0.1 mm wide, black; achenes dark brown, 4–5 mm long, marginal ones curved, narrowed at the calloused hollow base, gradually attenuate below the small (0.3 mm wide) pappus disk, 10-ribbed, ribs narrow,

rounded, smooth; pappus 4-5 mm long, white, 1-seriate, fine, soft, persistent. Flowers yellow.

N. Yunnan and W. Szechwan, montane.

Monomorphic.

Yunnan: Mt. Yülung-shan, near Lidjiang ("Likiang"), *Handel-Massetti 3615* (MW, UOf) type; Yangtze watershed, Prefectural dist. of Likiang, E. slopes of Likiang Snow Range, *Rock 4915*, July, 1922 (B, NY, US); Wei-si Hsien, *Wang 63952* (G). **Szechwan:** Baurong to Tatsienlu via Hadjaha, *Stevens 378* (B).

Relationship

Crepis elongata is very distinct from *C. tibetica* in the peculiar arrangement of the flower heads in cymose clusters of 2 to 4 heads usually on elongated peduncles; also in the shorter outer involucre bracts, smaller florets, and broader dark brown achenes. It is less close to *C. Gmelini* and *C. multicaulis*.

154. *Crepis multicaulis* Ledeb.

Fl. Altaica, 4: 125. 1833. (Pls. 21, 22. Figs. 232, 233.)

Perennial, 1-4 dm high, with short praemorse rhizome and fibrous roots; caudical leaves few, persisting, oblanceolate or elliptic, obtuse or acute, denticulate, dentate or remotely lyrate-pinnatifid with narrow triangular or oblong segments, tapering into a narrow winged petiole longer or shorter than blade and with clasping base, pubescent on both sides with yellow glandless setiform hairs or glabrate; cauline leaves 1-4, mostly bractlike; stems 1-3 (6) to a caudex, erect, slender, striate, glabrous or pubescent, simple or branched above with 1-8 corymbiform clusters of 2-8 heads; heads erect, with 30-40 florets; receptacle areolate, glabrous; involucre cylindrical before anthesis, 7-9 mm high, 2.5-3 mm wide at receptacle, ovate after anthesis; outer bracts 5-7, short; inner bracts 8-11, scarious-margined, ventrally glabrous, dorsally spongy-thickened at full maturity, ultimately strongly reflexed; corolla small, 5- or oftener 4-toothed, teeth thick, glandular; corolla tube densely pubescent with several-celled trichomes; anther tube short, yellow; style branches short, yellow; achenes reddish-brown, about 4 mm long, narrowly fusiform, subterete, attenuate to the narrow (0.15 mm wide) summit below the slightly expanded (0.2 mm wide) pappus disk, slightly attenuate to the yellow calloused hollow base, 10-12-ribbed, ribs narrow, nearly equal, ribs and interspaces densely and minutely spiculate; pappus white, about 4 mm long, 1-seriate, of rather numerous fine bristles, united at base, persistent but easily removed in sections. Flowering June-Aug.; flowers yellow.

Hieraciodes multicaule O. Kuntze, Gen. 1: 346. 1891.

N.E. Norway, mountains of Turkestan, the Altai and W. Himalaya regions; 1000-4000 m alt., except in Norway.

This widely distributed species comprises 2 well-marked subspecies which are connected by intergrading forms from the overlapping region of the two distributions.

Key to the Subspecies of *Crepis multicaulis*

Stem slender, glabrous or sparsely and finely gland-pubescent; peduncles divaricate; inflorescence open; involucre shortly gland-pubescent.....154, *a. genuina*

Stem stouter, densely gland-pubescent with setiform hairs; peduncles arcuate; inflorescence congested; involucre setulose with long glandular or glandless hairs.....154, *b. congesta*

154, *a. Crepis multicaulis genuina* (Rgl.) Babc., Univ. Calif. Publ. Bot. 19: 401. 1941. Plant rather small with horizontal or oblique rhizome; caudical leaves up to 9 cm long, 1.2 cm wide, dentate or obscurely lyrate, inconspicuously pubescent;

stems 1–2 to a caudex, more slender than in the next, glabrous or sparsely and finely gland-pubescent, branched only near top; peduncles 0.2–2.5 cm long, like involucre \pm canescent-tomentose and pubescent with dark green or mottled gland hairs; outer bracts 6–7, lanceolate, acute 1–3 mm long; inner bracts 8–10, lanceolate, obtuse or acute, 7–8.5 mm long; corolla about 7.5 mm long; ligule 0.6 mm wide; corolla tube 3 mm long; anther tube 1.6×0.8 mm dis.; appendages 0.5 mm long, acuminate; style branches 0.5 mm long. Chromosomes, $2n = 10$. See pl. 21 and fig. 232.

Crepis multicaulis var. *genuina* Rgl., ex Regel, Rach et Herder, Bull. Soc. Nat. Moscou, 32: 216. 1859.

C. multicaulis var. *laza* Rgl., Enum. Pl. Semen. in Bull. Soc. Nat. Moscou, 40 (3): 178. 1867.

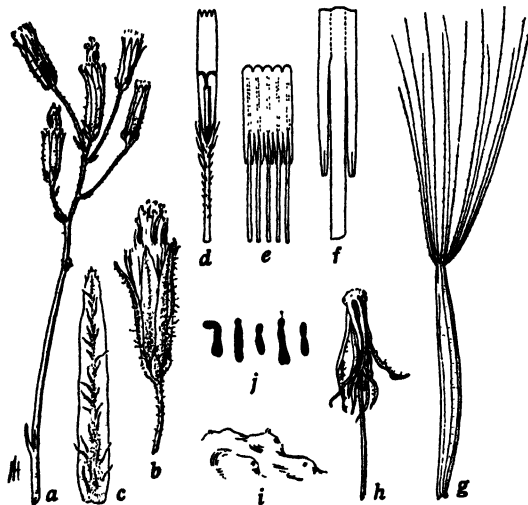


Fig. 232. *Crepis multicaulis typica*, a–f, from Fries in Herb. Norm. Scand. XV: 13 (K); g–i, from Fries in 1864 (FM); j, from hort. genet. Calif. 1480 (grown from seeds received from Copenhagen Bot. Gard.): a, aggregate inflorescence, $\times 1$; b, head after anthesis, $\times 2$; c, inner involucre bract, $\times 4$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, achene with pappus, $\times 8$; h, old head, $\times 2$; i, detail of receptacle, $\times 25$; j, somatic chromosomes, $n = 5$, $\times 1250$.

N.E. Norway, S. Siberia, Turkestan, Kashmir, Nepal. Type locality, as given by Ledebour, rocky island in the Tschuja R. opposite the mouth of the Kurai R. (presumably the Altai-Kurai reg.).

Plants from Norway are closely similar to the typical plants from the Altai reg. and Turkestan. More robust forms with somewhat larger leaves and more numerous and longer stems which occur in Turkestan and Kashmir are considered as intergradient between the subspecies (see minor variants).

Norway: Finmarken, mouth of Meskelfven R., among scattered trees, Fries in Herb. Norm. Scand. fasc. XV, no. 13 (K, B); E. Finmarken, Varanger, Aldjok, Fries in 1864 (FM); Finmarken, Nyborg, Balke in 1883 (FI); Finmarken, N. Varanger, Meskelfven, Haglund und Källström in 1899 (Bur). **Siberia:** Altai, Bunge, "from Bunge in 1837" (DC, K, B) probably isotypes; Altai, Maaschej R., Krylov in 1901 (G); Altai, source of Kanas R., Schischkin et al. in 1931 (NY). **Turkestan:** Ala-tau, Mt. Ala-tau, in gravel on the Lepsa, Sarchan, and Aksu rivers, Karelín and Kiriloff 1687 (K, NY, B); Kunghei Ala-tau, valley of the main Kabin R., alpine regions, Brotherus in 1896 (B); E. Turkestan, Sairam, 1000 m, Regel in 1877 (K, B) m.v. 1; Thian Shan, between Issyk kul and Mt. Musart, 1500–1800 m, Regel 704 (K) m.v. 1. **Kashmir:** Mt. Karakorum, 4242 m, Clarke 30208, (K) m.v. 2; Sonamarg, 3030 m, Stewart 6416 (NY) m.v. 3; Gurvaia, Clarke 29520 (K); Tangola, Purig, Koels in 1933 (US, NY, UC). **Nepal:** Kali Valley, Duthie 5718 p.p. (K, DD); Kutti Yangti Valley, Duthie 5718 p.p. (DD); Dhanli Valley, Duthie 5718 p.p. (DD) a robust variant. **Kumaun:** Kali Valley, near Kangua, Duthie 3089 (K).

Minor Variants of C. multicaulis genuina

1. Leaves up to 20 cm long, lyrate-pinnatifid, stems 2-5, branched lower down, obscurely pubescent below with pale glandular and glandless hairs. Possibly a hybrid between the subspecies. *Regel* in 1877 (K, B), Sairam, about 1000 m, E. Turkestan; *Regel* 704 (K), between Issyk kul and Mt. Musart, 1500-1800 m, Thian Shan, E. Turkestan.

2. Stems branched lower down; peduncles and involucre pubescent with yellowish gland hairs. *Clarke* 30208 (K), Mt. Karakorum, 4242 m, Kashmir.

3. Leaves lyrate-pinnatifid; stems purple and canescent-tomentose; peduncles densely tomentose and gland-pubescent. *Stewart* 6416 (NY), Sonamarg, Kashmir.

4. Robust garden plants, grown in Sweden. *Lund* in 1871 (FM), Christiania, Tojan; *Indebetun* in 1889 (Bur), grown from seed from Finmarken where it occurs "quasi subspontea" Christiania ♀

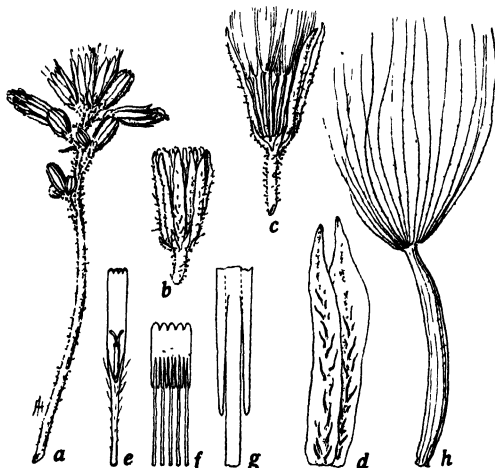


Fig. 233. *Crepis multicaulis congesta*, a-g, from *Gammie* in 1891 (K); h, from *Duthie* in 1892 (UWG): a, aggregate inflorescence of a small plant, $\times 1$; b, young head, $\times 2$; c, old head, $\times 2$; d, 2 inner involucre bracts, outer face, $\times 4$; e, floret lacking ovary, $\times 4$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, achene with pappus, $\times 8$.

154, b. *Crepis multicaulis congesta* (Rgl.) Bab., Univ. Calif. Publ. Bot. 19: 401. 1941. Plant rather robust with vertical or oblique rhizome; caudical leaves up to 13 cm long, 3 cm wide, conspicuously pubescent; stems 1-6 to a caudex, stouter than in the last, densely pubescent with yellowish glandular setiform hairs, branched sometimes below the middle; peduncles 0.2-1.2 cm long (sometimes up to 3.5 cm in cultivated specimens), densely tomentose and pubescent with short yellowish or mottled gland hairs; outer bracts 5-7, unequal, 1-2.5 mm long, lanceolate or ovate, acute, like inner bracts tomentose at base and gland-pubescent; inner bracts 8-11, lanceolate or oblong-attenuate, acute or obtuse, 7-9 mm long, pubescent with conspicuous yellow or green mottled glandular or glandless hairs: corolla about 6.5 mm long; ligule 0.6 mm wide; corolla tube 3 mm long; anther tube about 1×0.6 mm dis.; appendages 0.5 mm long, acuminate; style branches about 0.4 mm long. Chromosomes, $2n = 10$. See pl. 22 and fig. 233.

Crepis multicaulis var. *congesta* Rgl., Enum. Pl. Semen., in Bull. Soc. Nat. Moscou, 40(3): 178. 1867.

C. Stoliczkae C. B. Clarke, Comp. Ind. 255. 1876.

N.W. Himalaya reg. from the Alai Mts. south to Hazara, North-West Frontier Prov., and eastward into W. Tibet; 2600-4880 m. Type locality, Tien Shan on the Sary-Dshas R., 2727 m alt.

Nearly typical forms of this subspecies, except in respect to stature, predominate

among the specimens examined, but intergrading variants occur (see m.v. 5 and 6). The more robust habit is found even in the reduced forms first described by Regel. Although Regel's specimens of this subspecies were not seen, his brief description is definite in respect to stature, habit, and indumentum, and the locality is within the range of the subspecies. The low plants shown in pl. 22, *a*, therefore, are accepted as typical.

Turkestan: Alai Mts., near Olgin Lug, *Paulsen 439, 574* (B) m.v. 6. **Kashmir:** *Falconer 3029* (K); Lahul, upper Bhaga Valley on metamorphic rocks, *Stolicska* in 1878 (K); Tilail, *Clarke 30796* (K, Fl); Burjila, *Clarke 29871* (K); Baltistan, Thalle La, 4575–4880 m, *Stewart 20753* (UC); Baltistan, *Duthie 11605* (K, DD), *Duthie 11720* (Fl); Baltistan dist., Marpen Nullah, above Dras, *Duthie* in 1892 (UWG, DD); Baltistan dist., Dras Valley, *Duthie* in 1892 (B); Matayan, Dras, *Gammie* in 1891 (DD); above Astom Marg, *Drummond 14259* (K); Astom Marg, *Drummond 14309* (K) m.v. 5; Suru (?), *Meebold 976* (B); Wardwan, *Stewart* in 1912 (UC); Sonamarg, *Stewart 7246* (UC); Upper Lidar, Har Nag Pass, gravel, *Stewart 12388* (UC). **Punjab:** Kangra, Lahul, Drokpo Gongma, 4545 m, *Koels 6854* (US). **Tibet:** *Falconer 3646* (K). **North-West Frontier Prov.:** Hazara dist., Kagan Valley, *Inayat 19874* (K).

Minor Variants of C. multicaulis congesta

5. Peduncles 0.6–3.6 cm long and, like involucre, gland-pubescent with dark greenish mottled hairs. *Drummond 14309* (K), Astom Marg, 3636 m, Kashmir.

6. Peduncles and involucre merely tomentose, otherwise not pubescent. *Paulsen 439, 574* (B), among junipers near Olgin Lug, 2600–2800 m, Alai Mts., Kashmir

Relationship

Crepis multicaulis genuina has long been confused with *C. Gmelini*, with which it was supposed to intergrade through its larger forms. The two are very distinct, however, *C. multicaulis* being much smaller throughout, especially the corolla, which is less than half as long and usually with only 4 teeth, and the anther tube, which is only one-fourth as long and with different appendages. *C. multicaulis* is more similar morphologically to *C. tibetica* than to *C. Gmelini*; it is also related to *C. elongata*.

SECTION 22. PTEROTHECA

155. *Crepis sancta* (L.) Bab.

Univ. Calif. Publ. Bot. 19: 403. 1941. (Figs. 234-240.)

Annual, 0.3-5.5 dm high; root and caudex slender, or the caudex abruptly swollen, bearing few or many leaves and numerous stems; caudical leaves rosulate, 1-20 cm long, 0.5-4 cm wide, short- or long-petiolate, obovate, oblanceolate, or spatulate, obtuse or acute, denticulate, dentate, runcinate-pinnatifid, or lyrate, \pm pubescent with short yellow glandless hairs, or glabrescent; cauline leaves few, reduced, linear, mostly bractlike; stem or stems semidecumbent, strict, or erect,

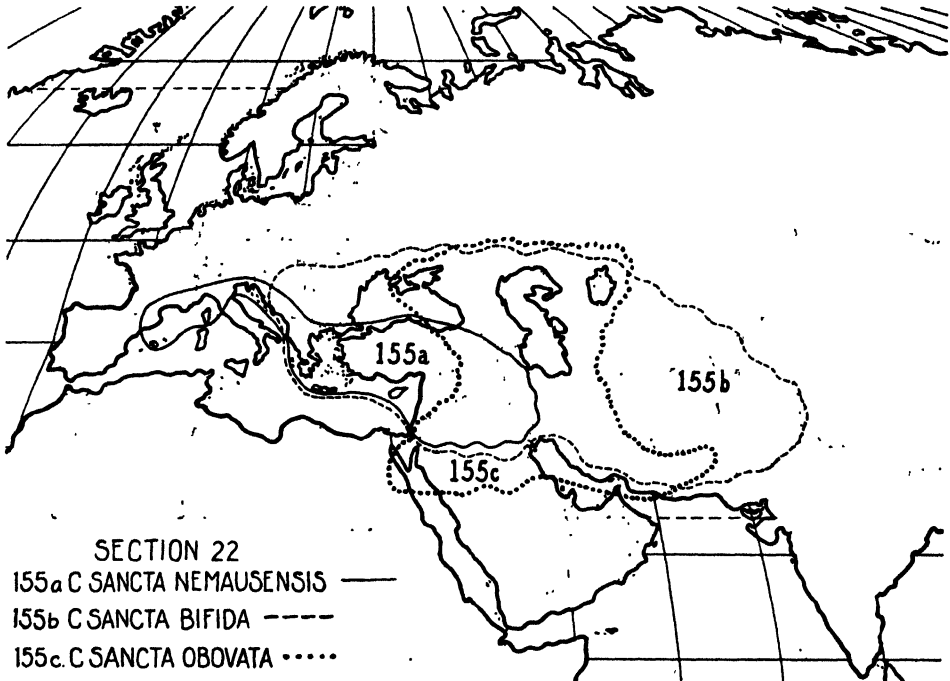


Fig. 234. Geographic distribution of the 3 subspecies of *Crepis sancta*, sec. 22. Based on Goode Base Map No. 201 HC. By permission of the University of Chicago Press.

very slender to robust, terete, \pm pubescent with yellow setiform hairs, or glabrous, simple and 1-headed, or dichotomously or cymosely branched usually above the middle or toward the summit and few- or many-headed; peduncles relatively long or short, slender, \pm pubescent with dark or pale hairs and with or without glands, or glabrous, near base of head often tomentose; heads erect, medium to small, 30-60-flowered; involucre cylindric, 6-11 mm long, becoming cyathiform or campanulate in fruit, ultimately reflexed, \pm tomentose and pubescent with dark or pale hairs or setules and with or without glands, or entirely glabrous; outer bracts 5-9 (11), nearly equal, ovate to linear, with membranous often conspicuous white margins; inner bracts 10-13, lanceolate, acute, with a narrow or broad white margin, glabrous on inner face, becoming strongly carinate and spongy-thickened dorsally in fruit; receptacle flat, paleaceous, the paleae setiform, yellow or brown, longer than the achenes but not exceeding the pappus, rarely absent; corolla yellow, sometimes with red on outer face of ligules; corolla tube $\frac{1}{4}$ - $\frac{1}{3}$ as long as the corolla, densely

pubescent with several-celled tortuous hairs; anther tube yellow; style branches green or yellow; achenes triform; outermost achenes (sometimes absent) from strongly alate to merely obcompressed or subterete but then usually 3-angled or with 3 stronger ribs; innermost achenes terete, slender, smooth; intermediate achenes terete, slender, coarsely or finely spiculate; pappus white, very fine and soft, scarcely exceeding the involucre.

Hieracium sanctum L., Cent. Pl. 2: 30. 1756; Amoen. Acad. 4: 328. 1759; Sp. Pl. ed. 2, 2: 1127. 1763, non Georgi.

Lagoseris sancta (L.) K. Maly, Glasnik zem. muzega u Bosni i Hercegovini 20: 556, 562. 1908 sens ampl. = *Pterotheca nemausensis* Bisch., Beitr. 241. 1851, *vide* Thell., Mém. Soc. Nationale Sci. Nat. et Math. Cherbourg, ser. IV, 38: 577. 1911–1912.

Mediterranean reg., especially countries to the north, east, and southeast, and eastward into N. India and Turkestan. Cf. fig. 234.

This polymorphic species is notoriously variable in such characters as size and habit of the plant, size and shape of the leaves, and number and size of the heads. Three well-marked subspecies can be distinguished, however, primarily on the basis of their characteristic marginal achenes and secondarily by differences in the width of the outer series of inner involucre bracts and by the color of the style branches. These three subspecies occupy different geographic regions, but their areas of distribution overlap in the E. Mediterranean reg., where intermediate variants occur, one of which has been shown by means of progeny tests to be of hybrid origin. Some of these intergrading variants can only be classified by placing them arbitrarily under the subspecies which they most nearly resemble. Although each of these subspecies has been recognized as a species by earlier systematists, there is good precedent, in their treatment by Thellung (*loc. cit.*), as well as by other authors, for merging them under one species. Furthermore, from a purely practical point of view, this is the most satisfactory treatment, because of (1) the difficulty in determining many specimens that lack mature achenes, (2) the occasional occurrence of specimens lacking the characteristic marginal achenes, (3) the occurrence of intergrading variants in certain localities.

The authoritative discussion of the nomenclature of this species given by Thellung (*loc. cit.*) makes it unnecessary to go into the matter exhaustively here. The only deviation from Thellung's treatment is the designation as *Crepis* of the species which he refers to *Lagoseris*. Also, the inclusion of subsp. *obovata* and of certain "species" as synonyms or variants under subsp. *bifida* is done here for the first time.

Key to the Subspecies of *Crepis sancta*

Fertile marginal achenes whitish, corticeous, strongly obcompressed, 3-alate or (in subsp. *bifida*) the alae sometimes obscure or lacking; style branches usually green.

Marginal achenes oblong to lanceolate, dorsally striate, the striae greenish, the lateral alae broad, thick, and soft in texture; outermost of the inner involucre bracts in flowering and young fruiting heads 1.2–2 mm wide (average 1.5–1.8 mm) 155, *a. nemausensis*

Marginal achenes linear-lanceolate, dorsally smooth, the lateral alae narrow, thin, and indurate (sometimes absent); outermost of the inner involucre bracts in flowering and young fruiting heads 0.8–1.5 mm wide (average 1–1.1 mm) 155, *b. bifida*

Fertile marginal achenes yellow, sometimes paler on ventral face, linear, subterete or obcompressed, ventrally 3-angled or with 3 stronger ribs, dorsally striate; style branches yellow 155, *c. obovata*

155, *a. Crepis sancta nemausensis* (Gouan) Thell., *loc. cit.* Stems numerous or few (sometimes only 1 in depauperate plants), mostly semidecumbent, 1–11-headed; heads mostly larger than in the other two subspecies; involucre dark green, some-



Fig. 235. *Crepis sancta nemausensis*, a-j, from Hall 12548 (UC 346478); k-n, from plant grown from Krause 3249 (UC 463870); o, from hort. genet. Calif. 3160 (grown from seeds collected near Beirut, Syria, by M. Zohary; cf. UC 466660): a, plant, $\times \frac{1}{2}$; b, detail of leaf, $\times 1$; c, old fruiting head, $\times 2$; d, head with involucre reflexed, $\times 2$; e-g, h-j, achenes from 2 plants (note that e bore no pappus, whereas h had a few setae and that i and j were drawn without pappus), $\times 8$; k, flowering head, $\times 2$; l, floret lacking ovary, $\times 4$; l', detail of ligule teeth, $\times 50$; m, anther tube, $\times 8$; n, detail of appendages, $\times 32$; o, somatic chromosomes, $n = 5$, $\times 1250$.

times 8 mm wide at the middle and usually \pm swollen in fruit; outer bracts ovate, acuminate, $\frac{1}{4}$ – $\frac{1}{3}$ as long as inner bracts; inner bracts often broader than in the other two subspecies, the outermost in flowering and young fruiting heads being 1.2–2 mm wide (average 1.5–1.8 mm); corolla 8–12 mm long; ligule 1–1.5 mm wide, the teeth 0.25 mm long; corolla tube about $\frac{1}{3}$ as long as the corolla; anther tube 2–3 mm long; appendages short, narrow, acuminate; filaments twice as long as the appendages; style branches about 1 mm long, very narrow, green; marginal achenes white with greenish dorsal striae, strongly obcompressed, corticeous, 3-alate, the lateral alae broad, thick, and soft in texture, the ventral ala thin, sharply edged. Flowering Jan.–July, mostly March–May. Chromosomes, $2n = 10$. See fig. 235.

Crepis nemausensis Gou., *Illus. Bot.* 60. 1773.

C. nuda Lamk., *Fl. Fr.* 2: 110. 1778.

Andryala nudicaulis Lamk., *Dict.* 1: 154. 1783.

A. nemausensis Vill., *Hist. Dauph.* 3: 66. t. 26. 1789.

Pterotheca nemausensis Cass., *Dict. Sc. Nat.* 25: 62. 1826–1834.

Lagoseris nemausensis Koch, *Syn.* 435. 1837 non M. B.

L. alata Nym., *Syll.* 50. 1854–1855.

Turkey, Syria, Palestine, and Iraq; Cyprus, Crete; here and there in the Balkan Pen.; N. Spain, S. France, and N. Italy; adventive in S. Germany, Switzerland, British Isles, Ukraine, Algeria, etc. The native habitat of this aggressive weed is probably Asia Minor, since it is widely distributed in that region and is genetically very close to subsp. *bifida*. Its comparatively recent introduction into N. Italy and its very rapid spread in that region are matters of record (cf. Sommier, S., *Bull. Soc. Bot. Ital.* 1900: 164–166). Hence, it seems very likely that it was introduced from Asia Minor into S. France.

Turkey: Bithynia, near Skutari, *Krause 3310* (UC); Mysia, Troja, Renkoei, *Ascherson 206* (B); Mysia, Sabandja, *Endlich 42* (B); Lydia, Smyrna, *Heldreich* in 1846 (B); *ibid.*, *Fleischer* in 1827 (K, B); Lycia, Myra, and Phineko, *Forbes* in 1876 (K); Galatia, Beybazar, *Aucher-Eloy 4896* (K); Turkish-Armenian border, south of Mt. Ararat, Bayazit (= Bayezid), *Aucher-Eloy 4856* (K); Marasch reg., Gaziantep (= Gazi Ayntap = Aintab), *Balls 2181* (UC); *ibid.*, Biredjik, *Sintenis 346* (B, Bo). **Syria:** Alexandretta, *Rogers 0611* (K); Antioch, *Rogers 0729* (K); Aleppo, *Kotschy* in 1841 (K); Beirut, in 1875, 1877 (K); Beirut, *Zohary* in 1931 (UC) m.v. 1; Saïda, *Gaillardet 1352* (K); Liban, Bicharre (= Beharra = Bsherre), *Miss Topali* in 1931 (UC) m.v. 1; west of Damascus, *Gaillardet* in 1816–1817 (B). **Palestine:** "south of Beirut," *Fox* in 1865 (K); near Deit Ballut, el Kafr, and Kibbiah, *Ogilvie* in 1919 (K); Jaffa, *Dinsmore 8380* (Co); Jerusalem, *Miss Gabrielith* in 1928 (K); Jerusalem, *Kenton* in 1871 (B); Tel-Aviv, *Zohary* in 1928 (K); Beersheba, *Lowne* in 1863–1864 (K); east of Dead Sea, Sar, *Meyers and Dinsmore* in 1911 (K). **Iraq:** Rum Kala'a, near the Euphrates, *Stapf* in 1888 (K); Port William, *Chesney* in 1836 (K); without locality, *Hausknecht* in 1867–1868 (B). **Cyprus:** near Kantara, *Sintenis and Rigo* in 1880 (K, B); Stavro Vouni, *Sintenis* in 1880 (B). **Crete:** Canea, *Sieber* (B) as *Apargia hyoseroides* Sieber, *Millina hyoseroides* DC.; Rettino, *Sieber misit*, 1821 (K, B) as *Crepis nudicaulis* Sieber. **Chios Is.:** *Guil* in 1931 (UC). **Greece:** Morea, *St. Vincent* in 1837 (B); Athens, *Spruner* (B); Macedonia, Bujanore, *Adamovic* in 1905 (B). **Croatia:** littoral, *Farkas* in 1896 (B). **Italy:** Rome and vicinity, *Honig-Jonas* in 1900 (B); Umbria, Liguria, *Lady Donie* in 1924 (K); Etruria, Ardenza, *Groves* in 1876 (K); Etruria, Firenze, *Fiori, Béguinot, and Pampanini* in 1904 (K). **Corsica:** littoral, *Wyate* in 1929 (K). **France:** Nice, *Talbot* in 1822 (K); Toulon, *Bourgeau* in 1848 (K); Marseille, Montredon, *Bourgeau* in 1848 (K); Avignon, *Requien* in 1818 (K); Montpellier, *Delile* in 1843 (B); Toulouse, *Timbal-Lagrange* in 1853 (K, B); Drome, Romans, *Hervier-Bassou* in 1871 (B); Pont du Gard, *Hall 12463a* (UC); Lyon, Limonest, *Hall 12548* (UC). **Balearic Is.:** Majorca, *Miss Edmonds* in 1929 (K).

Minor Variant of *C. sanota nemausensis*

1. Plant more like subsp. *bifida*; heads small, the involucre in fruiting heads 3–3.5 mm wide at middle, marginal achenes linear, with thin membranous alae; receptacle naked. Plants grown from seeds taken from the original specimen had similar habit and head size, but the achenes were more typical of subsp. *nemausensis*; the style branches were greenish-yellow instead of dark green as in

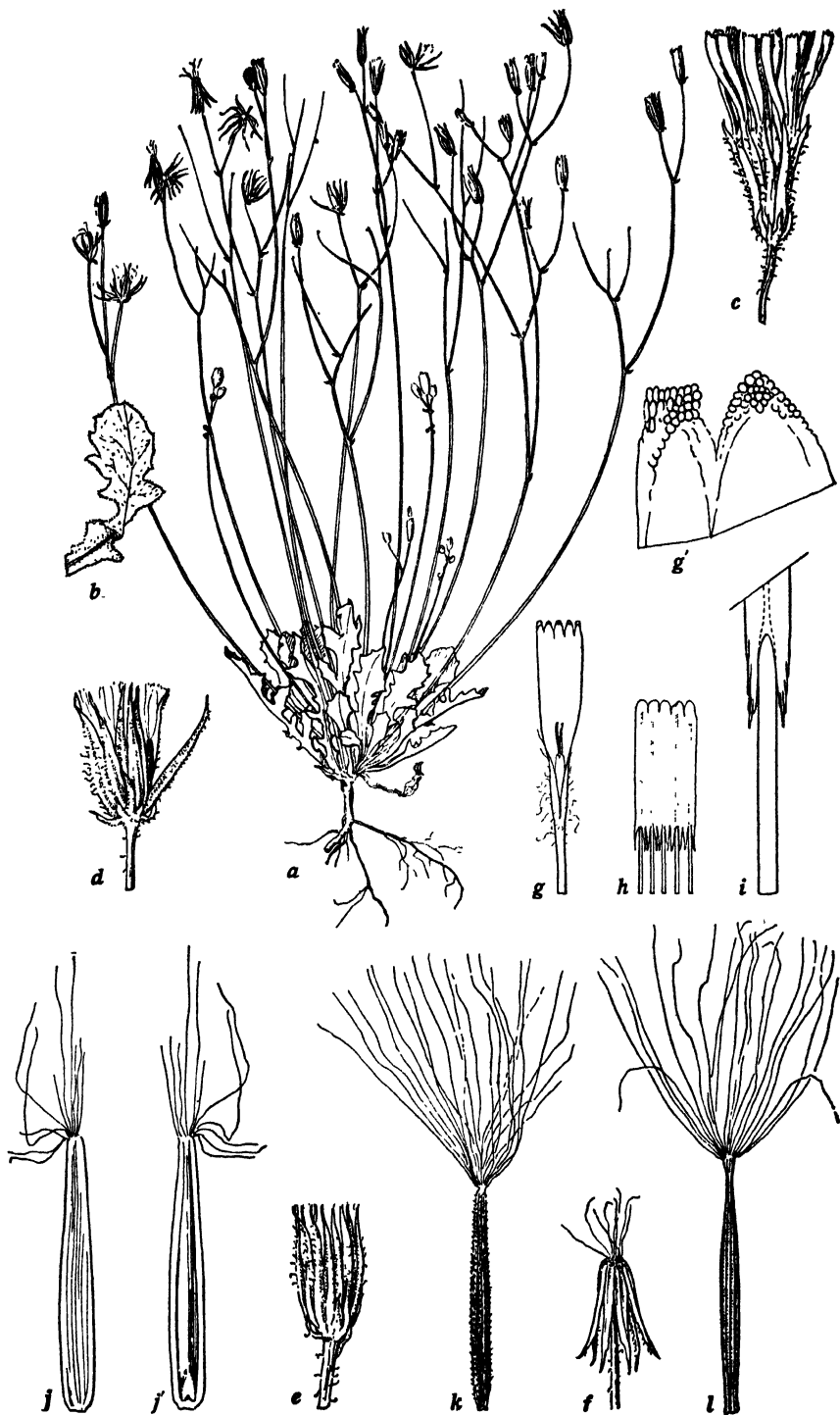


Fig. 236. *Crepis sancta bifida*, from Krause 3582 (UC 506847): a, plant, $\times \frac{1}{2}$; b, detail of leaf, $\times 1$; c, flowering head, $\times 2$; d, nearly mature fruiting head, $\times 2$; e, fully mature head, $\times 2$; f, head with bracts reflexed, $\times 2$; g, floret lacking ovary, $\times 4$; g', detail of ligule teeth, $\times 50$; h, anther tube, $\times 8$; i, detail of appendages, $\times 32$; j, j', k, l, outer achene, inner and outer faces, and 2 inner achenes, $\times 8$.

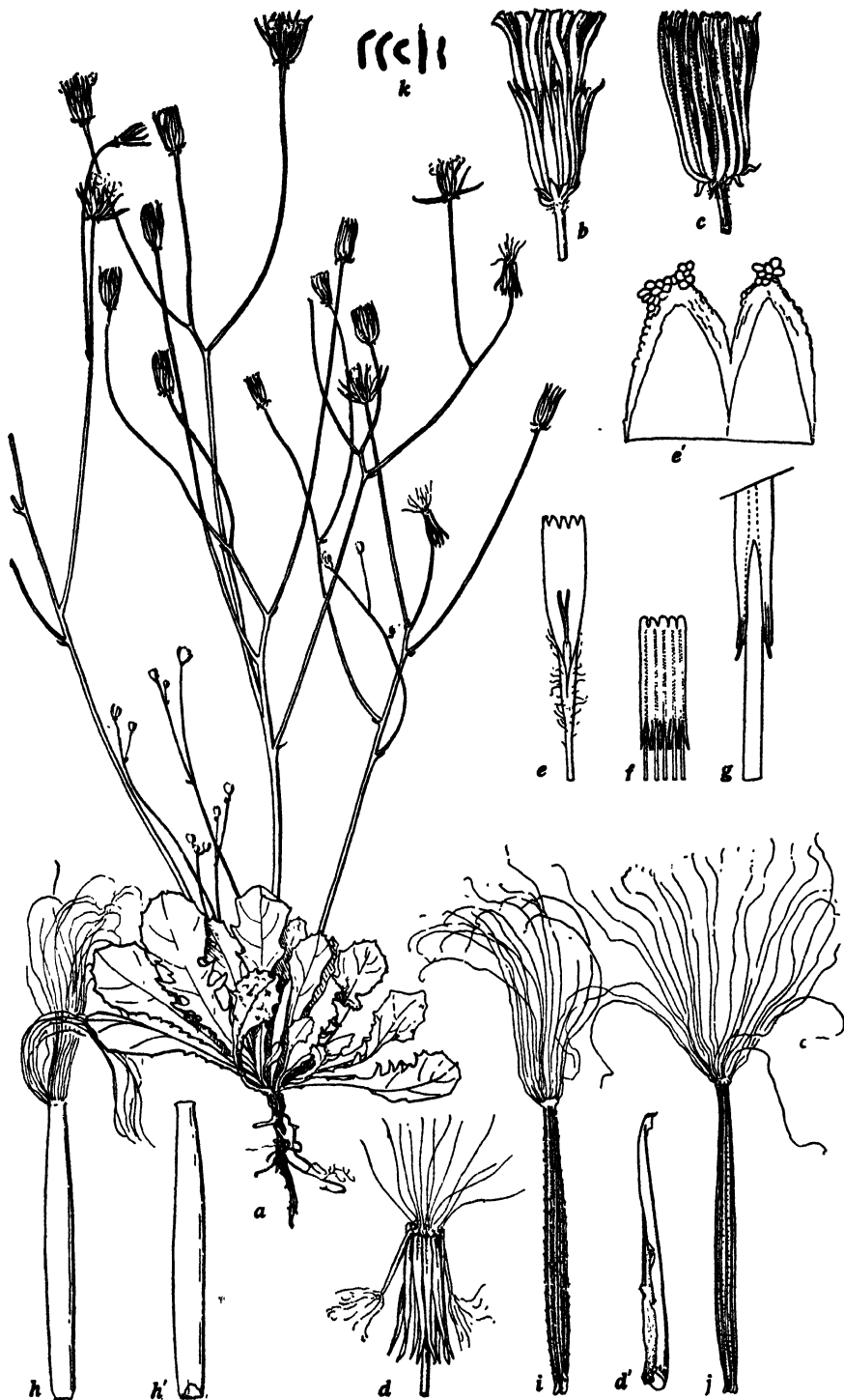


Fig. 237. *Crepis sancta bifida*, from hort. genet. Calif. 32.3087, grown from Krause 3393 (UC 506854): a, plant, $\times \frac{1}{2}$; b, flowering head, $\times 2$; c, old fruiting head, $\times 2$; d, head with bracts reflexed, $\times 2$; e, inner involucre bract, $\times 4$; e, floret lacking ovary, $\times 4$; e', detail of ligule teeth, $\times 50$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, h', i, j, outer achene, inner and outer faces, and 2 inner achenes, $\times 8$; k, somatic chromosomes, $n = 5$, $\times 1250$.

the parent plant; and the receptacle was naked. This is the only intermediate form between the subspecies of which it has been possible to make a progeny test; but the fact that intergrading forms occur at various places where subsp. *nemausensis* and *bifida* or *bifida* and *obovata* occupy the same area indicates that they hybridize naturally and the above-mentioned progeny test shows that such intermediate forms are fertile. *Miss Topali* in 1931 (UC) Bicharre (= Bcharrah = Bsherre), Lebanon, Syria; *Zohary* in 1931 (UC) near Beirut, Syria.

155, *b. Crepis sancta bifida* (Vis.) Thell., *loc. cit.* Stems numerous, few, or only 1 even in robust plants, mostly erect or strict, sometimes semidecumbent, 1-many-headed; heads extremely variable in size, mostly narrower than in subsp. *nemausensis* and longer than in subsp. *obovata*; involucre mostly light green, becoming stramineous in fruit, sometimes darker, up to 5 mm wide at middle in fruit, usually remaining nearly cylindric before becoming reflexed, sometimes \pm swollen; outer bracts deltoid to subovate, acute, $\frac{1}{8}$ – $\frac{1}{3}$ as long as the inner bracts; inner bracts often narrower than in subsp. *nemausensis*, the outermost in flowering and young fruiting heads being 0.8–1.5 mm wide (average 1–1.1 mm); corolla 7–13 mm long; ligule 1.5–1.75 mm wide, the teeth 0.1–0.6 mm long; corolla tube $\frac{1}{4}$ – $\frac{1}{3}$ as long as the corolla; anther tube 2–3 mm long; appendages less than 0.5 mm long, narrow, acuminate to obtuse; filaments 2–3 times as long as the appendages; style branches about 1 mm long, very narrow, usually green; marginal achenes white, smooth, \pm obcompressed, indurate, the 1 ventral and 2 lateral alae thick or thin, rounded at margins, the alate achenes rarely replaced with white non-alate ones, and very rarely both alate and non-alate white achenes occur in the same head. Flowering March–July, mostly April–May. Chromosomes, $2n \times 10$. See figs. 236–239.

Crepis nemausensis M. B., Fl. Taur. Cauc. 2: 255. 1808.

Lagoseris nemausensis M. B., Fl. Taur. Cauc. 3: 538. 1819.

Trichocrepis bifida Vis., Stirp. Dalm. 19 t. 7. 1826.

Pterotheca nemausensis C. A. Mey., Ind. Cauc. 58. 1831.

L. bifida Koch, Syn. 435. 1837.

P. bifida F. et M., Ind. IV Sem. Hort. Petropol. 43. 1837.

C. multicaulis C. Koch, Linnaea 23: 690. 1850 non Ledeb.

P. aralensis Bunge, St. Petersburg. Acad. Imp. VI a. Mém. Sav. Etr. 7: 383. 1851.

P. macrantha Bunge, *op. cit.* 384.

C. Kochii Tschihatch., As. Min. Bot. 2: 374. 1860.

L. Rueppellii Sch. Bip., Mus. Senk. 52. 1866.

C. Kochiana Boiss., Fl. Or. 3: 847. 1875.

L. orientalis Boiss., Fl. Orient. 3: 882. 1875 excl. *P. obovata*.

P. Falconeri Hook. f., Fl. Brit. Ind. 3: 399. 1882.

L. caspica Pacz., Florograph. and Phytogeogr. Invest. Kalmyk Steppes 90. 1892.

L. sancta (L.) K. Maly, *op. cit.* 556. *fide* Bornm., Bot. Jahrb. Beibl. 136: 122. 1926.

L. macrantha (Bunge) M. Ilin, Bull. Jard. Bot. Prin. U. R. S. S. 26: 416. 1927 ex descr.

P. caspica (Pacz.) N. Pavlov, Fl. Cent. Kazakstan III, no. 1464. 1938.

Throughout the Balkan states and the Aegean Archipelago, southern U. S. S. R., the Transcasian and Transcaucasian regions, Turkey, Syria, Palestine, Arabia, and eastward to Baluchistan, Afghanistan, Turkestan and the N.W. Himalaya reg.; from littoral situations to altitudes around 3000 m in the Himalayas.

Italy: Istria, near Pola, *Sendtner* in 1843 (K, B). **Hungary:** Swinitza, *Borbás* in 1874 (B). **Rumania:** Oltenia, *Nyárády* in 1930 (K). **Bulgaria:** near Varna, *Schneider* 211 (K, B). **Dalmatia:** Clissam, *Pichler* 196 (K, B). **Bosnia:** near Sarajevo, *Maly* in 1909 (B); *ibid.*, *Gilliat-Smith* 2693 (K). **Serbia:** near Pirot, *Adamovic* in 1897 (K). **Albania:** Moskopöl, 1272 m, *Alston and Sandwith* 2027 (K). **Greece:** central Arcadia and Attica, *Heldreich* in 1861 and 1894 (K); Thessaly, near Mt. Ossa, *Miss Topali* in 1938 (UC); Macedonia, Athos, *Hill, Sandwith, and Turill* 2421 (K); Crete, *Rettimo, Sieber* (K) as *C. nudicaulis*; Kalymnos, *Forsyth Major* in 1887 (K). **U. S. S. R.:** Crimea, Sebastopol, *Paczoski* in 1889 (Bo); Daghestan, *Becker* in 1874 (K); Georgia, Schusded, *Besser* (K); Armenia, Tchabantz Valley, *Koch* (B, UCf) as *Crepis multicaulis* C. Koch = *C. Kochii* Tschihatch.; *ibid.*, (Bo, UCf) as *C. Kochiana* Boiss.; Azerbaidshan,

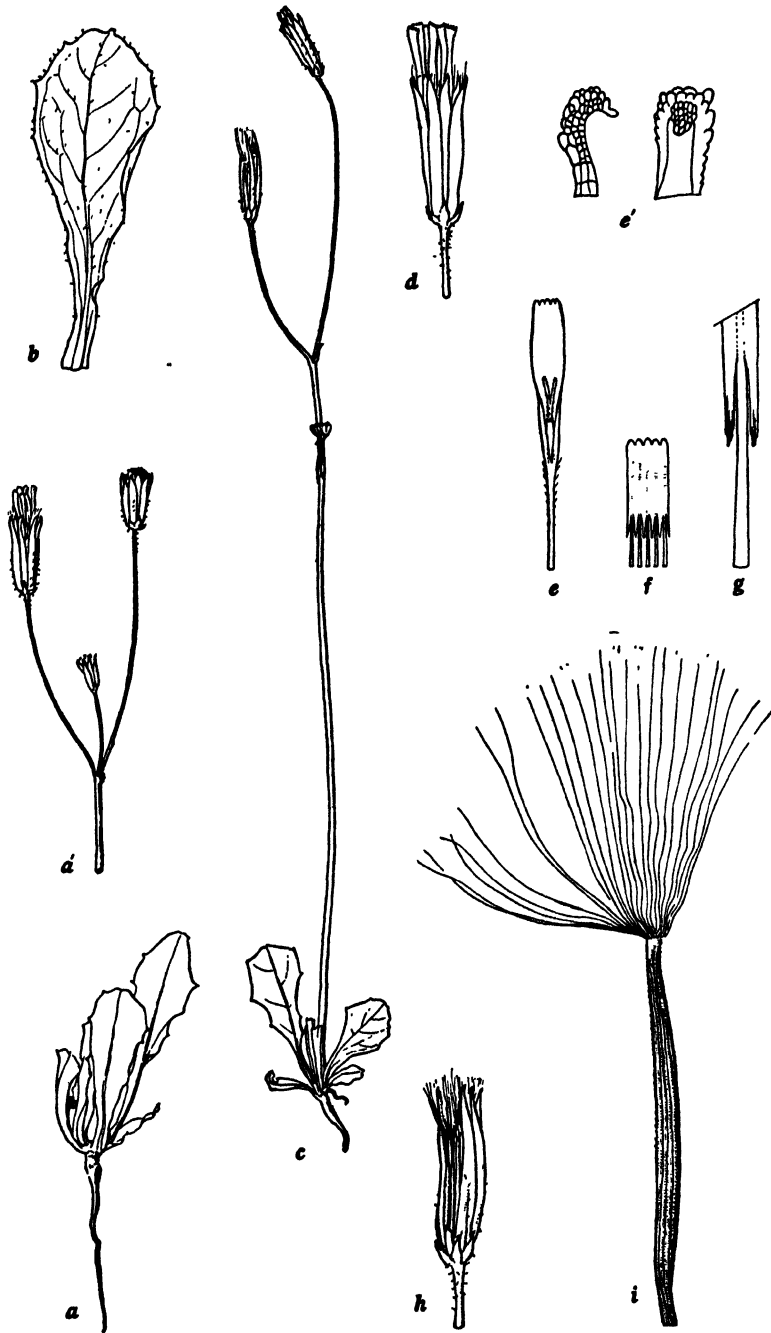


Fig. 238. *Crepis sancta bifida*, m.v. 2, from isotypes of *Pterotheca aralensis* Bge., Lehman (Bo, B): *a*, *a'*, parts of a plant, $\times 1$; *b*, leaf, $\times 2$; *c*, plant, $\times 1$; *d*, flowering head, $\times 2$; *e*, floret lacking ovary, $\times 4$; *e'*, detail of ligule teeth, $\times 100$; *f*, anther tube, $\times 8$; *g*, detail of appendages, $\times 32$; *h*, fruiting head, $\times 2$; *i*, achene with pappus, $\times 8$.

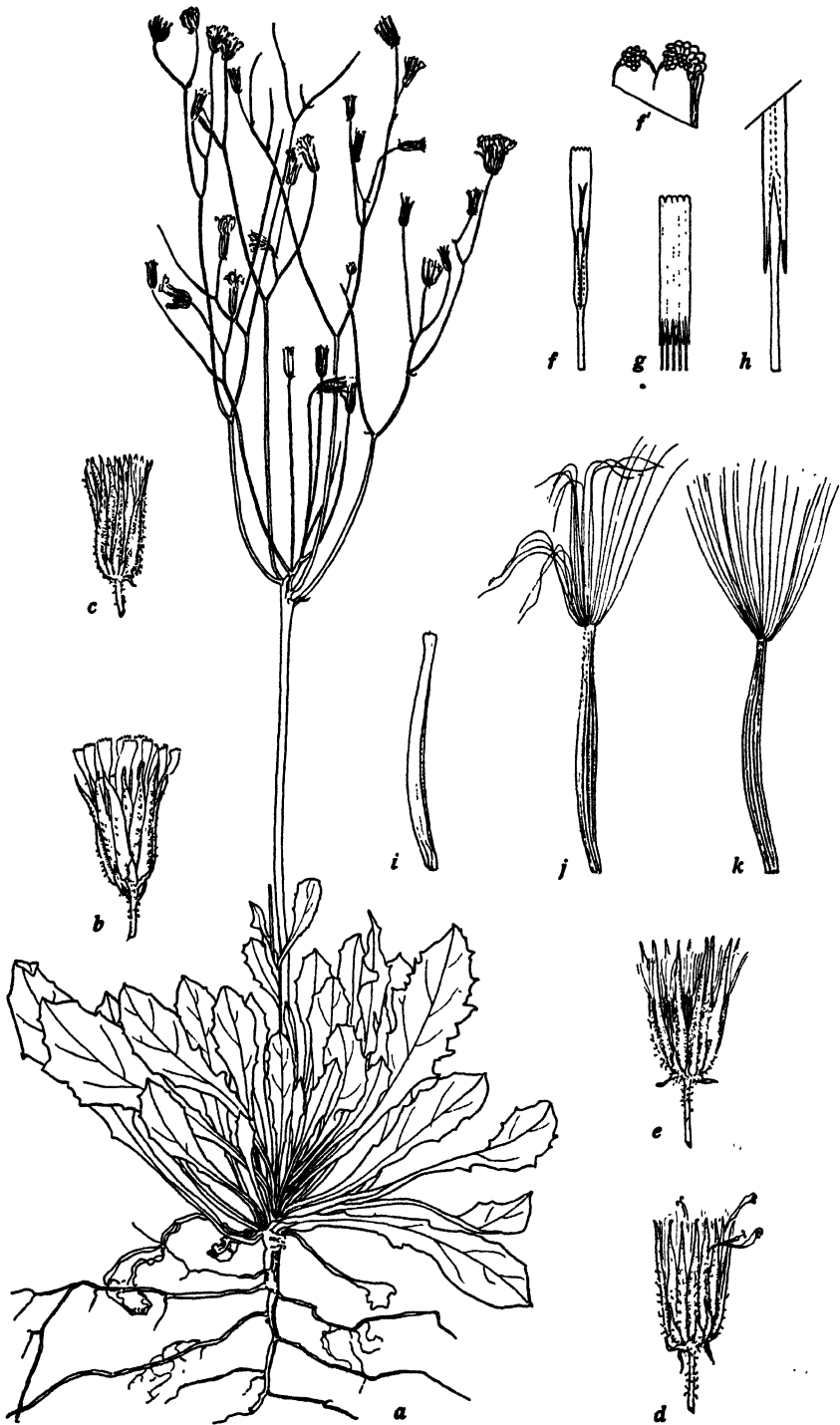


Fig. 239. *Crepis sancta bifida*, m.v. 3, a-c, from type of *Pterotheca Falconeri* Hook. f. (K); d-k, from *Mattiana* in 1888 (K): a, plant, $\times \frac{1}{2}$; b, flowering head, $\times 2$; c, immature fruiting head, $\times 2$; d, head after anthesis, $\times 2$; e, mature fruiting head, $\times 2$; f, floret lacking ovary, $\times 4$; f', detail of ligule teeth, $\times 50$; g, anther tube, $\times 8$; h, detail of appendages, $\times 32$; i-k, a marginal and 2 inner achenes, $\times 8$.

Aspheron Pen., near Bany, among rocks, *Karjagin* in 1933 (NY); *ibid.*, Kuba dist., 1600 m, abandoned field, *Karjagin* in 1935 (NY); Caspian desert, *Koch* in 1844 (B); Turkestan, *Bunge* (Bo, K, B) as *Pterotheca aralensis* Bge., cf. m.v. 2. Turkey: Gallipoli, *Kett* 132 (K); Trojan dist., *Schmidt* in 1864 (B); Galatia, Dikmen Dag, near Ankara, *Krause* 3552 (K, UC); Pontus, Amasia, *Bornmüller* 2717 (K, B); Pontus, Tokat, *Bornmüller* 3423 (K, B); Trebizond, Gumushkhane, *Bourgeau* in 1862 (K); Erzerum, *Huet de Pavillon* in 1863 (K); Cilicia, Bulgar Dag, Karli Bogas, 1800 m, *Siehe* 297 (K, B); Aintab, *Haussknecht* in 1865 (K); Urfa, near Kara-Pinar, *Sinten* 765 (B). Syria: Mesopotamia, Tell Halaf, *Seeman* in 1912 (B); Hammah, *Haradjian* 1853 (K); Zableh, *Post* in 1875 (K). Iraq: Mesopotamia, *Stapf* 765 (K). Persia: Tabriz, *Gilliatt-Smith*, K431, 1491, 1616, 1678, 1687, 1697 (K); Siaret, *Bunge* in 1858–1859 (K); Mandschil, *Pichler* in 1882 (K). Baluchistan: *Stocks* 837 (K); Surkhat Valley, 1818 m, *Lace* in 1889 (K). Afghanistan: Cabul, *Lemann* in 1852 (K); *ibid.*, *Griffith* 3353 (K); Hari-rud Valley, *Aitchison* 293 (K); Zarghan, *Duthie* (K). India: Kashmir reg., *Falconer* (K) as type of *Pterotheca Falconeri* Hook. f. = m.v. 3; *ibid.*, *Thomson* (K) m.v. 3; *ibid.*, *Edgeworth* in 1844 (K) m.v. 3; Kagan, Nilnadi, *Duthie* in 1897 (K) m.v. 3; Srinagar, *Stewart* 4091 (K) m.v. 3; Charval, *Gammie* in 1891 (K) m.v. 3; Pangl, *Lace* in 1890 (K) m.v. 3; Ramoo, *Clarke* 28474 (K); Ruttun Pir, *Clarke* 28264 (K); Shipiyu, *Clarke* 28616 (K); Hirpoor, *Clarke* 28712 (K); Liddar Valley, *Duthie* in 1901 (K); Pahlgam, *Stewart* 9198 (K); Punjab, *Kasanli* 25598 (K); Simla, *Gamble* in 1878 (K); Punjab, Kangra, Lahul, Kyelang, 3050 m, *Koelz* 5226 (US, UC) m.v. 3.

Minor Variants of *C. sancta bifida*

2. (*Pterotheca aralensis* Bunge, *loc. cit.*, fig. 238.) Plants depauperate; the caudical rosette very small; the single scapiform stem erect, slender, 1–3 headed; peduncles 1–3.5 cm long; involucre 10–12 mm long, 3–4 mm wide at middle; corolla about 9 mm long; ligule about 1 mm wide; anther tube about 1.5 mm long; style branches 0.5–0.75 mm long, yellow; achenes (immature) 7 mm long, apparently subterete, strongly attenuate near the summit, the outermost scabridulous, the inner smoothly (!) striate; pappus 5 mm long, white tinged with brown at the base. The type material (in herb. Boiss.) consists of a rosette and the upper part of a stem bearing 3 heads with flowers but no fruits. An isotype (in Herb. Berol.) is a single plant with 2 heads, one in flower and the other with partly mature achenes. A similar isotype (in Herb. Kew) has one head in flower. From this scanty material it is impossible to determine definitely the status of this form. Pavlov (348–350) maintains it as a species; but he states that D. I. Litvinov considers it hardly distinguishable from *P. bifida* F. et M., which is a synonym of *C. sancta bifida*. Pavlov (*loc. cit.*) maintains *P. macrantha* Bunge; but from Ilin's description (sub *Lagoseris*) it is obviously subsp. *bifida*. Pavlov also maintains *P. caspica* Pacz. (sub *Lagoseris*), although Ilin suggests that it is only a race of *P. macrantha*. Two other reduced forms, somewhat like *P. aralensis* Bunge, have been noted in herb. Boiss.; but they do not correspond with *P. aralensis* in certain characters. One was collected at Bogdo (Chinese Turkestan ?) by C. A. Meyer. It is similar in rosette, stem, and number of heads; but the involucre is only 9 mm long and the florets about 12 mm long; there are no fruits. The other was collected by Kowalensky in 1851 apparently in the Orient. It also has a very small rosette but bears 3 short stems, each dichotomously branched and bearing 2 heads on peduncles equal in length to the stem. Furthermore, the achenes are triformic, as in subsp. *bifida*, and of which it must be considered a reduced form. Citation of authentic material of *P. aralensis* Bunge is: *Bunge Bot. Lehm.* (Bo, K, B), *fide* Bunge (Mém. Ac. Imp. Sci. St. Petersb. par divers savants VII: 383. 1854) "on the dioritic hills between Juss-Chuduk and Bakali, April 25; in the old river bed of Jan-Darja, May 3; on the Aral steppe, May 17, 1842," Turkestan.

3. (*Pterotheca Falconeri* Hook. f., *loc. cit.*, fig. 239.) Plants often tall, with 1–7 erect or nearly erect stems, typically branched near summit, umbelliform, sometimes branched lower down, forming a compound cyme with several or many heads; heads mostly smaller than the average in subsp. *bifida*; corolla 7–8 mm long, the tube 2 mm long; ligule 0.75 mm wide; anther tube 2.5 mm long; style branches 0.6 mm long, green or black in sic.; achenes about 4 mm long, 0.3–0.4 mm wide; marginal achenes gray, obcompressed, striate on both faces, with narrow rounded lateral alae; the others brown, subterete or terete, striate, scabridulous or smooth. The marked tendency to robust habit, combined with smaller heads, florets, and achenes than are usually found in subsp. *bifida*, would seem at first to set this apart as a distinct subspecies; but typical subsp. *bifida* occurs commonly in the same area and intermediate forms also occur (sometimes on the same herbarium sheet typical subsp. *bifida*, m.v. 3, and intergrades may be seen). In the original description Hooker states: "I advance this species with much hesitation, for though differing in the achenes being all (sic!) terete and uniformly ribbed from *P. bifida*, I find so much variety in the outer achenes of that plant that I suspect this may prove to be a form of it." The *bifida*-like marginal achenes actually found in this form certainly confirm Hooker's suspicion. *Falconer* (K), without definite locality; *Thomson*, *Edgeworth*, (K), *ibid.*; *Duthie* in 1897 (K), Nilnadi, Kagan; *Stewart* 4091 (K), Srinagar; *Gammie* in 1891 (K), Charval; *Lace* in 1890 (K), Pangl, Kashmir reg.

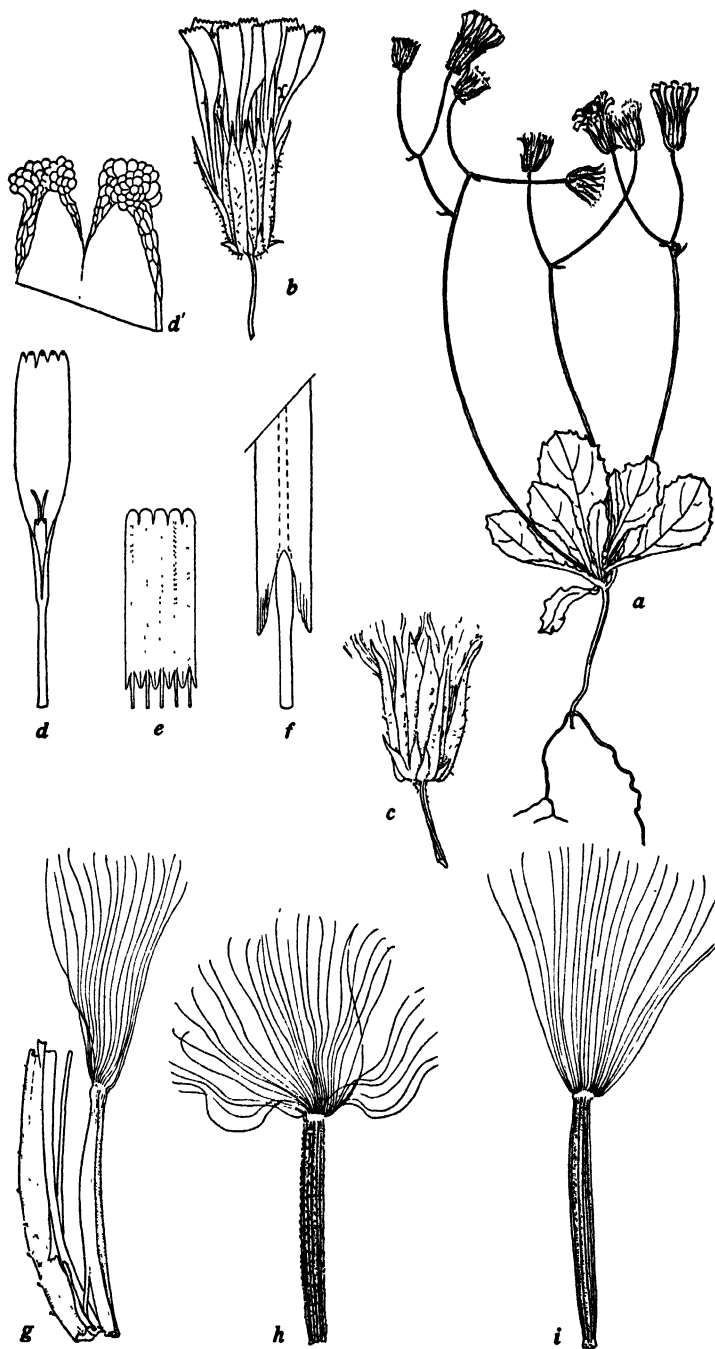


Fig. 240. *Crepis sancta obovata*, from type (Bo): *a*, plant, $\times \frac{1}{2}$; *b*, flowering head, $\times 2$; *c*, fruiting head, $\times 2$; *d*, floret lacking ovary, $\times 4$; *d'*, detail of ligule teeth, $\times 50$; *e*, anther tube, $\times 8$; *f*, detail of appendages, $\times 32$; *g*, inner bract and marginal achene, and *h*, *i*, inner achenes, $\times 8$.

155, c. *Crepis sancta obovata* (Boiss. et Noë) comb. nov. Stems 1–4, low, slender, 2–4-headed; heads smaller than in the other two subspecies; involucre light green, cylindric, 6–8 mm long, 3–5 mm wide at middle in fruit; outer bracts ovate, deltoid or linear, acute, $\frac{1}{8}$ – $\frac{1}{3}$ as long as the inner; inner bracts comparatively narrow, the outermost in flowering and young fruiting heads mostly less than 1 mm wide; corolla about 12 mm long; ligule 1.5–2 mm wide, the teeth 0.25–0.75 mm long; corolla tube $\frac{1}{4}$ – $\frac{1}{3}$ as long as the corolla; anther tube 3 mm long; appendages 0.4 mm long, narrow, acute; filaments about 0.3 mm longer; style branches 1.5 mm long, very narrow, yellow; marginal achenes yellow, 4.3 mm long, 0.3 mm wide, sometimes paler on ventral face, linear, subterete or obcompressed, ventrally 3-angled or with 3 stronger ribs, dorsally striate. Flowering March–May. See fig. 240.

Pterotheca obovata Boiss. et Noë, ex Boiss., Diagn. Pl. ser. 2, 3: 98. 1856.

Lagoseris orientalis Boiss., Fl. Orient. 3: 882. 1875 excl. *L. nemausensis* M. B. and *Crepinia Marshalliana* Rehb. = nom. nud.

Upper Egypt, Sinai Pen., and adjacent Arabia, Palestine, Syria, Caucasus reg., E. Turkey, W. Turkestan, Iran, and Baluchistan; probably in Iraq. The type locality, "in subalpinis Armeniae meridionalis circa Ardana," probably refers to a village in the Kurdistan reg. of S.E. Turkey or N.W. Persia. The inclusion of the Caucasus, Crimea, and Caspian regions in the distribution of this species is based on Pavlov (III. no. 1466).

Egypt: middle Egyptian desert, Arabian side, S. Galata, 1050–1300 m, *Schweinfurth 53, 178* (Bo, K, B). **Arabia:** Sinai Pen., foot of Mt. Sinai, *Schimper 409* (Bo, CA, K); Sinai reg., Beian, *Drake* in 1870 (K); central Midian = El Hidjas, *Barton* in 1878 (K). **Palestine:** "Arabia Petraea" = Transjordan south, Petra, *Boissier* in 1846 (Bo); *ibid.*, *McDonald* in 1849 (K); Tell Fara = Tell el Fare (†) near Beersheba, *Harding 243* (K). **Turkey:** S. Armenia, around Ardana, subalpine (= Kurdistan reg. †), *Noë* in 1852 (Bo) type. **Persia:** between Abuschir and Schiras, near Gere, *Kotschy* in 1842 (Bo); Kerman Prov., hills near Kerman, about 2000 m, *Bornmüller 4142* (Bo); N. Persia, *Pichler* in 1882 (Mo) m.v. 4; near Schahrud, *Bunge* in 1858 (Bo). **Baluchistan:** *Stocks* (G.)

Minor Variant of *C. sancta obovata*

4. Plant more robust, with 3–7 stems, about 15 cm high; involucre 8–9 mm long; outer bracts deltoid; style branches green. This form appears to show some effects of previous hybridization between subsp. *obovata* and subsp. *bifida*. In the same herbarium there are two collections of Stapf, probably from either Persia or Syria, which show still more resemblance to subsp. *bifida*, so much in fact that they may be arbitrarily placed in that subspecies, although their delicate slender stems, very small heads, and the *obovata*-like achenes of one of them show the influence of the latter subspecies. The two plants designated as m.v. 4 were collected by *Pichler* in 1882 (Mo), in N. Persia.

Relationship

Crepis sancta exhibits close resemblance to *C. multicaulis* in its chromosomes, the two widespread subspecies of *C. sancta*, namely subsp. *nemausensis* and subsp. *bifida*, having almost identical karyotypes. But morphologically, *C. sancta* shows more resemblances to sec. 16, especially to *C. purpurea*, in habit, leaf shape, involucre, flowers, fruits, and the receptacular paleae. The likeness in floral characters includes such details as the extremely fine pubescence of the corolla tube, the delicate anther tube with very fine filaments, and the almost linear anther appendages. Unfortunately, the species of sec. *Lagoseris* have not been examined cytologically, but it seems fairly likely that they have 5 pairs of chromosomes and a karyotype similar to that of *C. sancta*, although *C. connexa* may have 6 pairs. At any rate, the most obvious relations of *C. sancta* are with sec. 16; and its geographic distribution fits perfectly with the conception that it was derived from either an existing or an extinct species of *Lagoseris*.

SECTION 23. ZACINTHA

The 4 species in this section exhibit a considerable range in degree of primitiveness or advancement as determined by comparative morphology. Yet they resemble one another more than the species of any other section, not only in habit of the plant and in leaf shape but most notably in the involucre and achenes. There is a marked tendency throughout the group for the involucre to become strongly indurate, enclosing the achenes; and in the more advanced species the involucre becomes more or less constricted above the achenes so that the marginal ones at least are strongly curved. By comparing the illustrations of these species in the order presented these marks of an evolutionary trend within the group will be obvious.

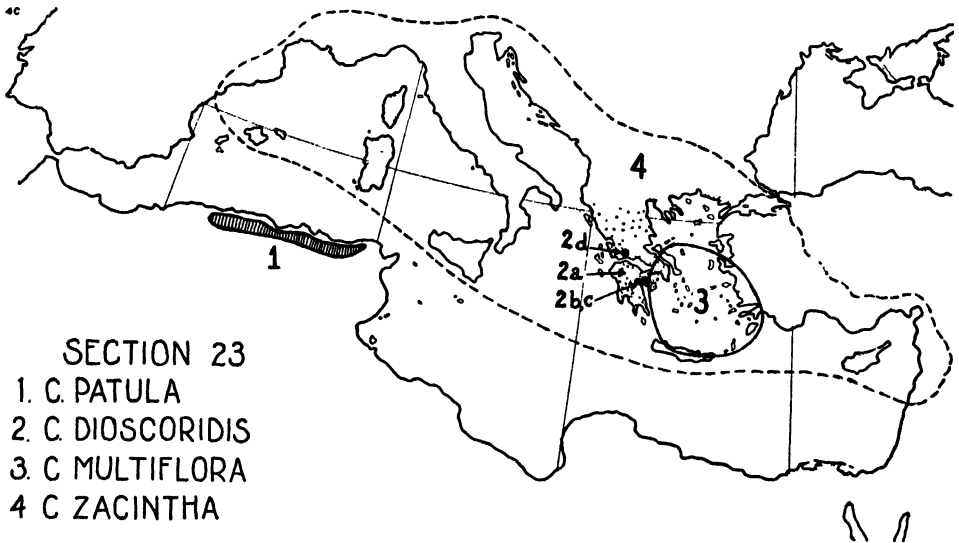


Fig. 241. Geographic distribution of the 4 species in sec. 23. The single stations for *C. Dioscoridis* subsp. *argolica*, *tyrinthica*, and *tubaeformis* are shown by small solid circles; subsp. *typica* (2a.) is widespread in Greece. Based on Goode *Base Map No. 124*. By permission of the University of Chicago Press.

C. patula, an endemic of N. Algeria and Tunisia (cf. fig. 241), is a strong-rooted, moisture-loving perennial. Its short, thick, vertical taproot bears many fibers in which respect this species resembles *C. Reuteriana* of section 19 and, like it, *C. patula* may be considered a connecting species between the advanced deep-rooted species and the primitive rhizomatous species of this genus. Other evidence that *C. patula* is much more primitive than the other three species is found in the larger, less specialized involucre, and the larger florets and achenes. The achenes especially are interesting because, although they are much less specialized than in the other three species, yet they do show a definite tendency toward the modifications which have become so marked in the advanced species. The extremely short, hardly noticeable pappus is another feature of unusual interest. Apparently this reduction of the pappus almost to the vanishing point has gone along with the indurate involucre which completely encloses the achenes. Unquestionably *C. patula* is much older than the other three species. If its present geographic distribution is considered in relation to the center of distribution for the group, which is in the Balkan Pen., and then, if the distribution of this section is considered in relation to the assumed center of origin of the genus in Central Asia, it follows logically that *C. patula*, or

its parent form, was widely distributed in the Mediterranean region in ancient times. Either *C. patula* was the immediate ancestor of the other three species or they all descended from a common ancestor.

The other three species are annuals. *C. Dioscoridis* stands next to *C. patula* in primitiveness. It is restricted to Greece and surrounding islands in its indigenous distribution but it is adventive in other Mediterranean countries. In Greece there are three local races of this species which have become so sharply differentiated from one another that they are treated here as subspecies, even though it is not likely that they are well isolated from one another. One of these, subsp. *argolica*, shows the closest resemblance to *C. patula*. Apparently it represents an early stage in the evolution of the group. From this point two lines diverge. One of these lines leads to *C. Dioscoridis typica* and thence to the much more advanced *C. multiflora*. The other includes *C. Dioscoridis tirynthica* and *C. Dioscoridis tubaeformis*; and the highly specialized *C. Zacintha* probably arose from this line. That *C. Zacintha* is a very successful species, in spite of (or because of ?) its tightly closed involucre, is shown by its wide distribution in the Mediterranean reg. (cf. fig. 241). It is also adventive in N. Africa.

The chromosomes of these species are in general agreement with the foregoing hypothesis. All of the species have 4 pairs of generally similar chromosomes, except *C. Zacintha* which has 3 pairs. No cytogenetic research has yet been conducted on this interesting group of species, except within *C. Dioscoridis*; although attempts have been made to hybridize *C. Zacintha* with *C. Dioscoridis*, thus far without success.

Key to the Species of Section 23

- Plant perennial; involucre in fruiting heads 12–14 mm long, 4–8 mm wide; achenes uniform, 20–30-ribbed; pappus extremely short, 0.2–0.4 mm long. 156. *C. patula*, p. 743
- Plant annual; involucre in fruiting heads 6–12 mm long, 5–10 mm wide; achenes biform, the marginal laterally compressed, winged or angled, the inner 4–8 ribbed; pappus 1–5 mm long.
- Peduncles bearing fruiting heads inflated toward the summit, constricted at base of head; corolla 11–18 mm long; anther tube 3–6 mm long; style branches 1.5–2.5 mm long. 157. *C. Dioscoridis*, p. 745
- Peduncles bearing fruiting heads not inflated; corolla 7–8 mm long; anther tube 2.5 mm long; style branches 1–1.5 mm long.
- Involucres becoming ovoid in fruit, not strongly indurate; outer bracts 8–12, subulate; style branches yellow; inner (discal) achenes dark brown; pappus 3.5 mm long 158. *C. multiflora*, p. 758
- Involucres becoming turbinate in fruit, strongly indurate; outer bracts 5, lanceolate; style branches green; inner (discal) achenes yellowish; pappus 1.5 mm long. 159. *C. Zacintha*, p. 760

156. *Crepis patula* Poir.

Voy. Barb. 2: 227. 1789. (Fig. 242.)

Perennial, 2–4.5 dm high; caudex short, stout, woody, 0.7–2 cm wide, bearing many strong somewhat fleshy fibers at the base, or sometimes elongated into a stout woody furcate fiber-bearing rootstock up to 4 cm long, leafy at crown, with many persistent brown indurate bases of old leaves; caudical leaves 5–20 cm long, 1.5–4 cm wide, oblanceolate, mostly obtuse, runcinately dentate to lyrate pinnatifid, with triangular or roundish lobes, attenuate to a short or elongated winged petiole, thickish, glabrous or finely pubescent with short pale glandless hairs; cauline leaves few, remote, lowest one or two similar to caudical leaves or, like the others \pm reduced, sessile, uppermost often bractlike; stems of preceding season sometimes persisting; stems of the season 1–2, erect, terete, striate, canescent-tomentulose or tomentose

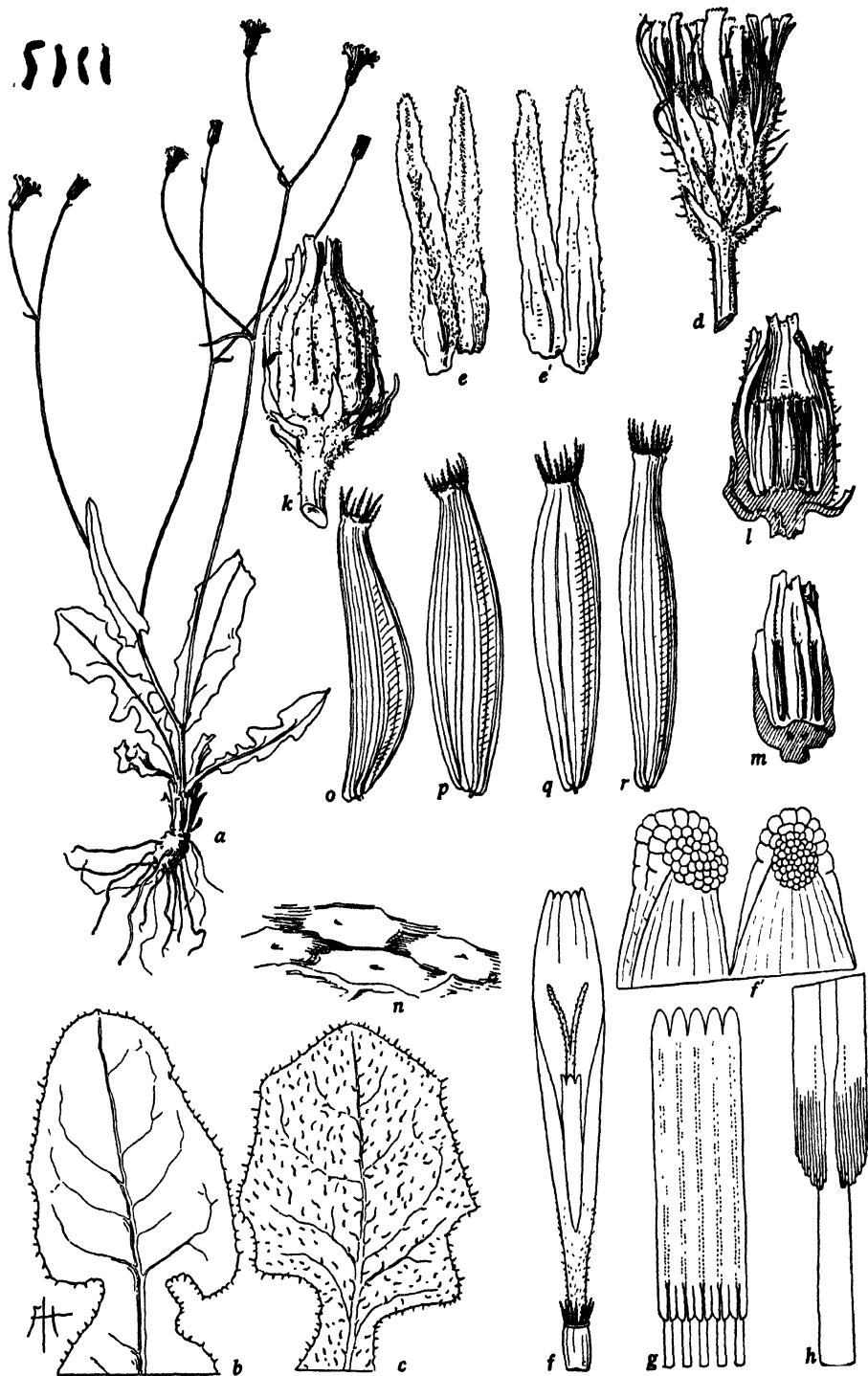


Fig. 242. *Crepis patula*, from Babcock 258 (UC 429454): *a*, plant, $\times \frac{1}{4}$; *b*, apical part of cauline leaf, lower face, $\times 1$; *c*, *ibid.*, upper face, $\times 1$; *d*, flowering head, $\times 2$; *e*, 2 inner involucral bracts united, outer face, $\times 4$; *e'*, *ibid.*, inner face, $\times 4$; *f*, floret, $\times 4$; *g*, anther tube, $\times 8$; *h*, detail of appendages, $\times 32$; *k*, mature head, $\times 2$; *l*, *ibid.*, longitudinal section, $\times 2$; *m*, 4 united inner bracts from same, showing thickened, indurate receptacle and bracts, $\times 2$; *n*, detail of receptacle, $\times 25$; *o-r*, 4 achenes, $\times 8$; *s*, somatic chromosomes, $n = 4$, $\times 1250$.

at bifurcations, 1-headed or remotely 1-3-furcate beginning near base, branches elongated, divaricate or arcuate, 1-3-headed; peduncles 6-24 cm long, stiffly upright, tomentulose below, tomentose and slightly thicker near head in fruit; heads erect, medium, about 50-flowered; involucre cylindric, becoming urceolate in fruit, 12-14 mm high, 4-5(8) mm wide at middle in fruiting heads, canescent-tomentose and \pm setulose with black or whitish setules with or without glands; outer bracts 10-14, unequal, longest $\frac{1}{2}$ as long as the inner, lance-linear or linear, acuminate, like inner bracts rounded at the white-ciliate apex; inner bracts 12-14, lanceolate, acute, finely appressed-pubescent on inner face, becoming rounded-carinate and dorsomedianly pale spongy-thickened at early maturity, the whole involucre ultimately strongly indurate and persistent enclosing the achenes; receptacle areolate, punctate, glabrous; corolla in marginal florets about 15 mm long; ligule 2.5 mm wide near middle, 1.25 mm at summit; teeth 0.25-0.4 mm long; corolla tube about 3 mm long, pubescent with acicular hairs 0.1-0.25 mm long; anther tube about 5.5×1.5 mm dis.; appendages 0.65 mm long, oblong, obtuse; filaments 0.75 mm longer; style branches about 3 mm long, 0.15 mm wide, entirely yellow or yellow with green hairs; achenes light brown, 5-6 mm long, 1-1.4 mm wide, subterete or 4-angled, abruptly attenuate near the apex, 0.4-0.5 mm wide just below the white unexpanded pappus disk, constricted at the lightly calloused closed base, 20-30-ribbed, ribs narrow, close, rounded, smooth, nearly equal, or 4 or 5 definitely stronger, or some marginal achenes flattened but carinate on ventral face with one median and two marginal ribs much stronger; pappus white, 0.2-0.4 mm long, 1-seriate, barbellulate, deciduous. Flowering Apr.-June; flowers yellow. Chromosomes, $2n = 8$.

Lapsana virgata Desf., Fl. Atl. 1: 235. 1798-1800.

Ceramioccephalum patulum Sch. Bip., Bull. Soc. Bot. Fr. 9: 284. 1862.

Hieraciodes patulum O. Kuntze, Gen. 1: 346. 1891.

E. Algeria and N. Tunisia, mostly near the coast and in adjacent mountains, in moist situations, often among or near trees or shrubs. Endemic.

In lieu of any other specimen of Poiret, the sheet in herb. Lamarck (Paris) which bears the label, "*Crepis patula* D. Poiret" in Lamarck's script, may be accepted as the type. The material apparently consists of parts of one plant in a fair state of preservation. No locality is given with this specimen and Poiret cites no locality in his description; but Desfontaines (*loc. cit.*) states that his material was sent by Poiret and that it came from La Calle, and Schultz Bipontinus (*loc. cit.*) refers to La Calle as the classic locality.

Monomorphic.

Algeria: La Calle, Poiret (P in herb. Lamarck) type; La Calle, Durieu in 1841 (PC) as *Lapsana virgata* and *Ceramioccephalum patulum*; La Calle, in a grove or thicket, Clavé in 1920 (UC); Constantine, Seuhadja, Cosson in 1861 (P); Prov. Constantine, Dukerley in 1863 (B); vicinity of Algiers, forest of *Quercus suber* at Ait Kalfoua, Battandier and Trabut 174 (DL, PD); E. Algeria, Grand Kabylie, near Yakouren, edge of grove of *Quercus suber*, moist loam, partial shade, 300 m, Babcock 258 (UC). **Tunisia:** Kroumirie, Dj. Bir, near Ain Draham, Cosson et al. in 1883 (P, B); north of Ferrara, Camp de la Santé, Cosson et al. in 1883 (P).

Relationship

Crepis patula is outstanding because of its extremely reduced pappus borne on rather large, many-ribbed achenes which are fairly primitive in type. As an endemic relic it stands as a connecting link between the other more advanced members of this section and more primitive ancestors which probably resembled such species as the more primitive members of sec. 10, especially *C. Strausii* and *C. Raulini*.

But in its medium-sized heads highly specialized involucre and extremely reduced pappus, *C. patula* has become a considerably more advanced species. On the other hand, it exhibits strong resemblances to the other species in this section, especially to *C. dioscoridis argolica*, in habit and leaf shape, and considerable resemblance in the achenes. Furthermore, *C. Zacantha*, the most advanced species of this section, has a still more extreme development of the closed, indurate involucre. The suggestion of Schultz (*loc. cit.*) that *C. patula* shows affinity with *Billotia* (= *C. alpina*) is rather far-fetched, since both involucre and achenes, as well as life span, habit, and leaf shape are very different in the two species.

157. *Crepis Dioscoridis* L.

Sp. Pl., ed. 2, 1133. 1763. (Figs. 243–247.)

Annual or biennial, monocarpic, 1–6 dm high, erect, divaricate or decumbent; root slender to stout and woody; caudex very narrow to \pm swollen and divided at summit; caudical leaves ephemeral, 4–15 cm long, 1–3 cm wide, lanceolate to oblanceolate, acute or obtuse, denticulate to pinnatifid with 6–8 broad triangular lateral segments, the terminal segment relatively large or small, petiolate or sessile, glabrous or sparsely pubescent with short pale glandless hairs; cauline leaves mostly or all sessile, amplexicaul, acutely auriculate, lanceolate, acute or acuminate, denticulate; peduncles arcuate, flexuous or erect, 1–25 cm long, slender near base, becoming broader toward summit, \pm constricted near the head, fistulose, glabrous, tomentulose, gland-pubescent or sparsely setulose; heads erect, small to medium, 25–70-flowered; involucre cylindric in anthesis, becoming globose in fruit; canescent-tomentulose, gland-pubescent or setulose; outer bracts linear, unequal, the longest $\frac{1}{3}$ – $\frac{1}{2}$ ($\frac{2}{3}$) as long as the inner; inner bracts 10–14, lanceolate, acute or acuminate, ventrally glabrous, becoming incurved and strongly convex dorsally, enclosing the marginal achenes; receptacle areolate or alveolate with low fimbriae, glabrous or sparsely ciliate; corolla yellow, 11–18 mm long; anther tube yellow, 3–6 mm long; style branches yellow, 1.5–2.5 mm long, attenuate toward tip; achenes 3.5–5.5 mm long, biform or (subsp. *tubaeformis*) uniform; marginal achenes strongly curved, laterally compressed, dorsally convex, ventrally concave and mostly broadly alate, \pm attenuate to summit and base; inner achenes similar or different in color, \pm curved or nearly straight, subcompressed to subterete, attenuate to both ends or shortly and coarsely beaked, regularly or irregularly ribbed or angled; pappus white, 1–5 mm long, 2-seriate, fine to extremely fine, caducous or deciduous.

Indigenous in Greece, where it is common in waste places, especially in the southern half of the country, at lower and submontane elevations.

This species, although polymorphic, is represented throughout most of its range by forms which more or less closely resemble the Linnaean type (fig. 243, *a*). However, there also exist, at 3 localities in the south of Greece, 3 different forms which are so distinct morphologically from the typical forms and from one another that they are treated here as subspecies. As will be noted below, one of these forms (subsp. *tubaeformis*) was originally described as a species by Halacsy. Since the other two are equally distinct, the present author was at first inclined to treat them also as species. In support of such a treatment it might be argued that the very existence of such distinct forms in the same geographic area with typical forms would indicate that they are isolated either ecologically or physiologically. Furthermore, it has been found by experiment that it is characteristic, in subspp. *tubaeformis* and *argolica*, for the individual plant to be more or less self-fertile. This, of course, would tend to preserve racial differences, especially when any sort of isolation exists. There is some indication that one of these subspecies (*argolica*) may be

isolated both ecologically and physiologically in nature. On the other hand, subsp. *tubaeformis* has evidently hybridized naturally with typical *C. Dioscoridis* and produced a population composed of individuals exhibiting various combinations of the parental characters. No evidence is yet available concerning the present distribution of the third subspecies (*tirynthica*), but ecologically it does not appear to be isolated from subsp. *typica*, because specimens of the latter have also been received from Tiryns and one of these proved to be a hybrid (see below). It must be emphasized, however, that at present each of these three local forms is known from only one locality, and nothing is known concerning their range of distribution in their respective districts. Also, the karyotype of all three local forms is practically identical with that of typical *C. Dioscoridis*. This fact and the high fertility of the intersubspecific hybrids indicate that the genetic differences involved must be in the nature of genic or very small structural changes.

Experimental crosses made by F. L. Smith (unpublished) between typical *C. Dioscoridis* and subsp. *argolica* produced hybrids which were as highly fertile as the parental forms. This is in striking contrast with the rather low fertility of hybrids between *C. Dioscoridis typica* and *C. multiflora* (q.v.). Experimental crosses with the typical *C. tubaeformis* Hal. could not be made, since the only living plants available were descendants of the natural hybrids mentioned above. About one hundred of these were grown at Berkeley in 1932. Although cultivated under uniform conditions, these offspring exhibited much variation, especially in habit. Several individuals approached closely to the habit type of *C. Dioscoridis typica*, and one was found that approached the type of subsp. *tubaeformis*.

Evidence that subsp. *tirynthica* crosses naturally with subsp. *typica* and differs from it with respect to certain genes was obtained as follows: A specimen of subsp. *typica* was collected by Costopolos at the same locality as the type of subsp. *tirynthica*. Seeds from this specimen (hort. genet. Calif. 3038) produced a few plants, one of which was protected and allowed to self-fertilize. It produced only subsp. *typica* achenes. From the few selfed seeds obtained 5 plants were grown the following year. These plants exhibited sharp segregation in color, shape, and size of the achenes. In one plant the achenes were exactly like those of subsp. *typica*; two others had achenes just as characteristic of subsp. *tirynthica*; whereas in the remaining two the achenes showed different combinations of subspp. *typica* and *tirynthica* characters. In one plant the achenes were like subsp. *typica* in shape and size but pale in color like subsp. *tirynthica*; in the other they were intermediate in size and like subsp. *tirynthica* in shape, but the inner ones were dark brown, as in subsp. *typica*. Such sharp segregation among so few plants indicates a simple genetic basis for these achene differences. But since subsp. *tirynthica* differs from subsp. *typica* as well as from subsp. *argolica* in many morphological details, it is safe to assume that it differs also in a good many genes.

Further study of this interesting species, both in the field and in the experimental garden, is highly desirable. In view of the available evidence, the present taxonomic treatment appears to be justified.

Key to the Subspecies of *C. Dioscoridis*

Involucre in fruiting heads 7–10 mm wide; marginal achenes strongly alate, 1.5–2 mm wide, (occasionally absent in subsp. *typica*); pappus 3–5 mm long.

Plant erect, central axis elongated and stronger than the branches; inner (discal) achenes reddish-brown, 10-ribbed, ribs narrow, spiculate.....157, *a. typica*

Plant prostrate, decumbent or divaricate, central axis absent, very short or scarcely stronger than the branches; inner (discal) achenes yellow or greenish, sometimes irregularly angled, mostly 4–8-ribbed, ribs broad, smooth.

Plant prostrate or decumbent; involucre glandular-pubescent; pappus exceeding the involucre at maturity; marginal achenes whitish; inner achenes pale greenish-yellow, irregularly angled and ribbed 157, *b. argolica*

Plant divaricately branched from base; involucre shortly setose, glandless; pappus shorter than the involucre at maturity; achenes all greenish-yellow, the inner ones strongly 4-5-ribbed 157, *c. tiryinthica*

Involucre in fruiting heads 5-6.5 mm wide; achenes all pale yellow or (in variants supposed to be hybrids with subsp. *typica*) some or all of the achenes brownish and rugulose; marginal achenes about 1 mm wide; pappus 1-2 or 3 mm long 157, *d. tubaeformis*

157, *a. Crepis Dioscoridis typica* Babc., Univ. Calif. Publ. Bot. 19: 400. 1941. Annual, 1.3(6) dm high, root slender; caudex simple, narrow; caudical leaves up to 15 cm long, 3 cm wide, oblanceolate, denticulate to lyrate-pinnate with broad triangular lateral lobes and broad deep sinuses, gradually attenuate into a winged petiole; lower cauline leaves mostly lanceolate, acuminate, sessile, amplexicaul, auriculate or lacinate at base; stem erect or somewhat flexuose, central axis stronger than the branches, glabrous, remotely branched from near base or below middle upward, branches elongated, dichotomously few-branched, aggregate inflorescence corymbiform; peduncles arcuate, 1-13 cm long; heads 50-70-flowered; involucre 8-10 mm long, 7-9 mm wide at middle in fruit; outer bracts 6-8, dark green, $\frac{1}{3}$ as long as the inner; inner bracts 12-14, dorsally setulose and gland-pubescent, the glands brown, or merely tomentulose; receptacle shallowly alveolate, sparsely ciliate; corolla about 15 mm long; ligule 2.5 mm wide; teeth 0.75 mm long; corolla tube 4.5 mm long, pubescent with minute acicular hairs; anther tube 6×1.5 mm dis.; appendages 0.8 mm long, lanceolate, acute; filaments 0.4 mm longer; style branches 1.5-2 mm long, 0.1-0.15 mm wide; achenes 4-5.5 mm long, marginal whitish or yellowish, 1.5-2 mm wide, dorsally convex, laterally 2-grooved and 2-alate, ventrally nearly straight with a broad thin median wing; inner reddish-brown, 0.5-0.75 mm wide, 10-ribbed, ribs narrow, spiculate; pappus conspicuously extruded, 4-5 mm long. Flowering April-June; ligules reddish on outer face. Chromosomes, $2n = 8$. See fig. 243.

Crepis Dioscoridis L., Sp. Pl., ed. 2, 1133. 1763.

C. tomentosa Moench, Meth. 535. 1794 et *C. patula* Desf., Tabl., ed. 1, 88. 1804 *vide* DC., Prod. 7: 172. 1838.

C. globifera Hall. f., Naturw. Anzeig. 1: 19. 1818.

C. croatica Horn., Hort. Hafn. Suppl. 90. 1819.

C. heterosperma Schrad., ex Sprengel, Syst. Veg. 3(2): 635. 1825.

Gatyna globulifera Cass., Dict. Sc. Nat. 18: 185. 1827.

G. Dioscoridis Rehb., Fl. Germ. Exc. 254. 1830-1832.

Picris globifera Desf., Hort. Par. Cat. ed. 2, 1832.

Endoptera Dioscoridis DC. (*loc. cit.*)

G. Bergeri Sch. Bip., Flora 22: 21. 1839.

C. Bergeri Steud., Nom. Bot., ed. 2, 436. 1840.

Hieraciodes Dioscoridis O. Kuntze, Gen. 1: 346. 1891.

Throughout Greece and adjacent islands, but less frequent in the N. half. Adventive in Crete, Dalmatia, Italy, France, Switzerland, Germany, and Hungary.

Variations occurring in nature, so far as they are represented in the herbarium material examined, consist mainly in differences in size of the plant, which may often express merely differences in environmental effects. The only significant morphological variation noted among herbarium specimens is the occasional absence of the characteristic marginal achenes. Crossing experiments have shown that this difference has a simple genetic basis. Under cultivation, however, this subspecies has been prolific in genic variations. Among the new Mendelian characters which have come to light are such striking qualitative differences as "apricot" flower color

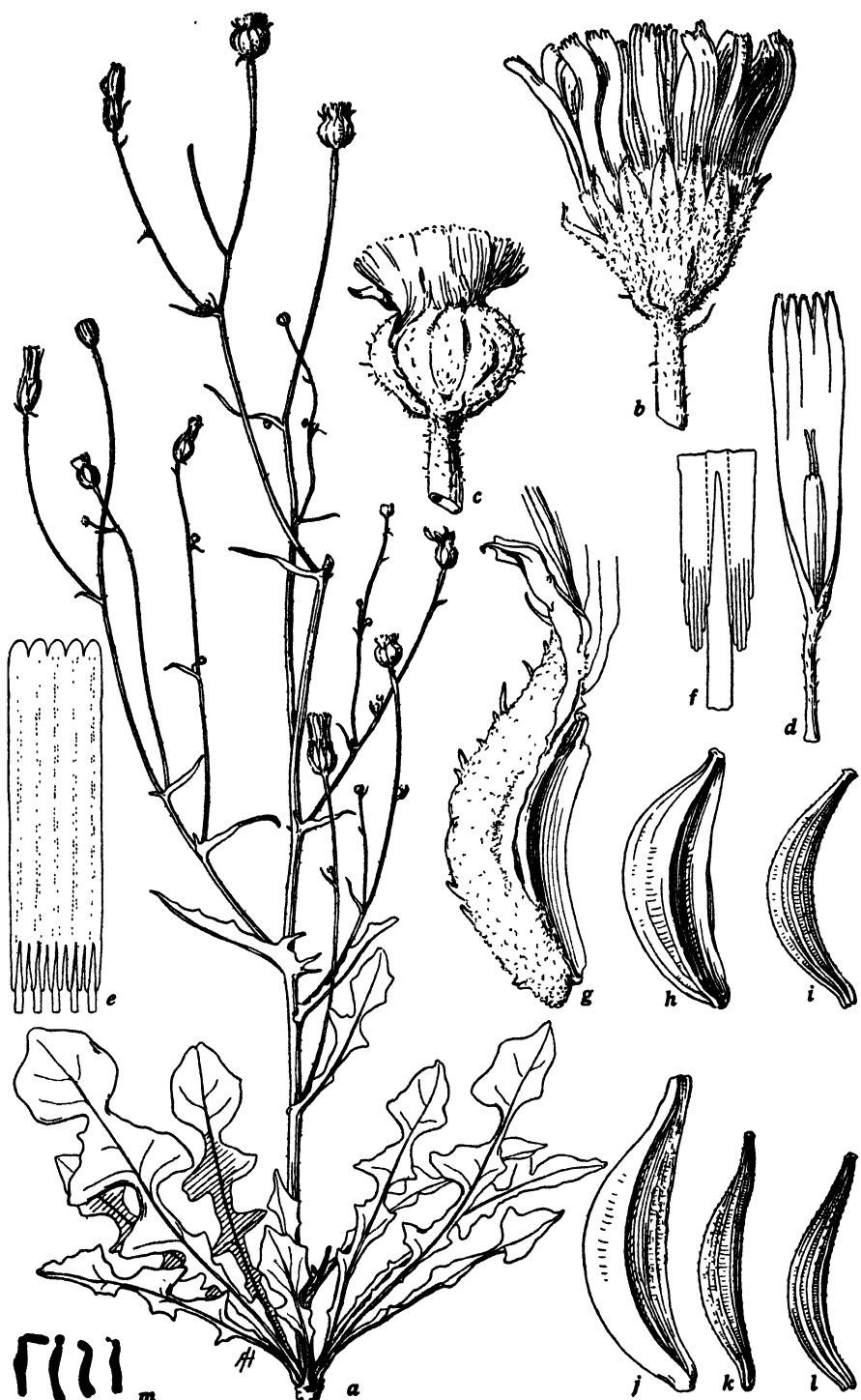


Fig. 243. *Crepis Dioscoridis typica*, a, from type (L); b-f, from hort. genet. Calif. 27.1631-11 (UC 602787); g-i, from Heldreich in 1847, Nauplia, Greece (B); j-l, from type of *Endoptera Dioscoridis* (DC); m, from hort. genet. Calif. 1455 (grown from seeds received from Dr. G. Poirault, Villa Thuret, Antibes, France; cf. UC 676611): a, plant, $\times \frac{1}{2}$; b, c, heads, $\times 2$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, involucre bract enclosing achene, $\times 8$; h, i, marginal and inner achenes, $\times 8$; j-l, marginal and 2 inner achenes, $\times 8$; m, somatic chromosomes, $n = 4$, $\times 1250$.

and "yellow" herbage, both of which are recessive to the normal wild type. Furthermore, a strain (1174) derived from seeds collected on Mt. Hymettus at 880 m by Demades in 1921 (see specimens cited below) was found to be distinct from other cultivated strains in that the plants were shorter and more bushy and matured more slowly. It was also found that seeds of this strain required a rest period, whereas the others germinated promptly. Finally, it was reported by Navashin (unpublished) that the satellite on the D chromosome is larger in this strain than in typical strains. But the original specimens of Demades, although very variable in size, are not distinct morphologically from typical *C. Dioscoridis*. In other words, on Mt. Hymettus at an altitude of 880 m, there exists a strain which is a distinct genetic entity but which has not become sufficiently differentiated morphologically under natural conditions to warrant taxonomic recognition. The plants occurring at lower levels on Mt. Hymettus (see de Heldreich no. 1354) may or may not belong to this same strain.

The critical specimens examined consisted of the type in the Linnaean Herb. (sheet no. 18, a photograph of which is in Herb. UC), and several folios in herb. DC, among which are specimens bearing most of the synonyms listed above.

Greece: Attica, Mt. Hymettus, near Karyes, 300 m, *Heldreich 1354* (Bur); Mt. Hymettus, 880 m, *Demades* in 1921 (UC); Attica, Mt. Lycabettus, *Heldreich* in 1873 (B); Corinthia-Argolis, Nauplia, *Heldreich* in 1874 (B); Corinthia-Argolis, Tiryns, *Costopulos* in 1931 (UC); Arcadia, Megalopolis, *Costopulos* in 1931 (UC); Laconia, near Sparta, *Babcock 324* (UC); Laconia, near Mt. Taygetos, *Heldreich* in 1844 (B); Messenia, Pylus, *Heldreich* in 1844 (B); Morea, Elis, Kyllene, *Bretzl* in 1905 (UC); Corfu, *Bicknell* in 1891 (Bur); Thessaly, Mt. Olympus, *Guiol* in 1929 (UC); Crete, Rethymo, *Gandoger 5178* (Mo). **Dalmatia:** Lissa I., *Pichler* in 1872 (B). **France:** Bouches-du-Rhone, *Reynier* in 1902 (Bur); Marseille, Aubagne, *Hall 12500* (UC).

157, b. ***Crepis Dioscoridis argolica*** Bab., Univ. Calif. Publ. Bot. 19: 400. 1941. Annual or biennial, 1–1.5 dm high or higher, decumbent; root stout, woody; caudex short, \pm swollen, divided at summit; caudical leaves disappearing before flowers appear (in cult. up to 14 cm long, 2.5 cm wide, oblanceolate, pinnate, terminal segment small and ovate, petiolate, glabrescent); cauline leaves mostly sessile, linear, acutely auriculate or bractlike; stems several, short, divaricate, dichotomously branched near base, branches long, widely spreading, arcuate, 1–3-furcate or pedunculate; peduncles 4–13 cm long (in cult. much longer); heads 50–70-flowered; involucre 9–11 mm long, 7–10 mm wide in fruit, gland-pubescent, the glands purple; outer bracts 6–8, purplish; inner bracts 12, gray-green with dark purple dorsal stripe; receptacle shallowly alveolate, glabrous; corolla 11 mm long (in cult. up to 18 mm); ligule 2(3) mm wide; teeth 0.3–0.8 mm long; corolla tube 5 mm long, sparsely pubescent with stout 2–4-celled acicular hairs up to 0.3 mm long; anther tube (3)4 \times 1.2 mm dis.; appendages 0.5–0.6 mm long, oblong, truncate; style branches 2–2.5 mm long, 0.15 mm wide; achenes 3.5–5 mm long, marginal whitish, 2 mm wide, dorsally convex, laterally 2-grooved and 2-alate, ventrally concave with a broad thin median wing, contracted toward summit, each ala prolonged beyond summit as a short spine, inner pale greenish-yellow, irregularly angled and ribbed, ribs smooth, strongly calloused at base, contracted into a very short coarse beak; pappus copious, 3–3.5 mm long, slightly exceeding the involucre. Flowering May–June; ligules reddish on outer face and red-tipped. Chromosomes, $2n = 8$. See fig. 244.

Known only from the type locality.

Greece: Argolis, Bay of Argos, near Nea-Kios, south of Argos, gravelly strand 10–15 m above upper limit of high tide, among herbs, *Babcock 322* (UC) type and isotypes; loc. class., *Guiol 1322* (UC).

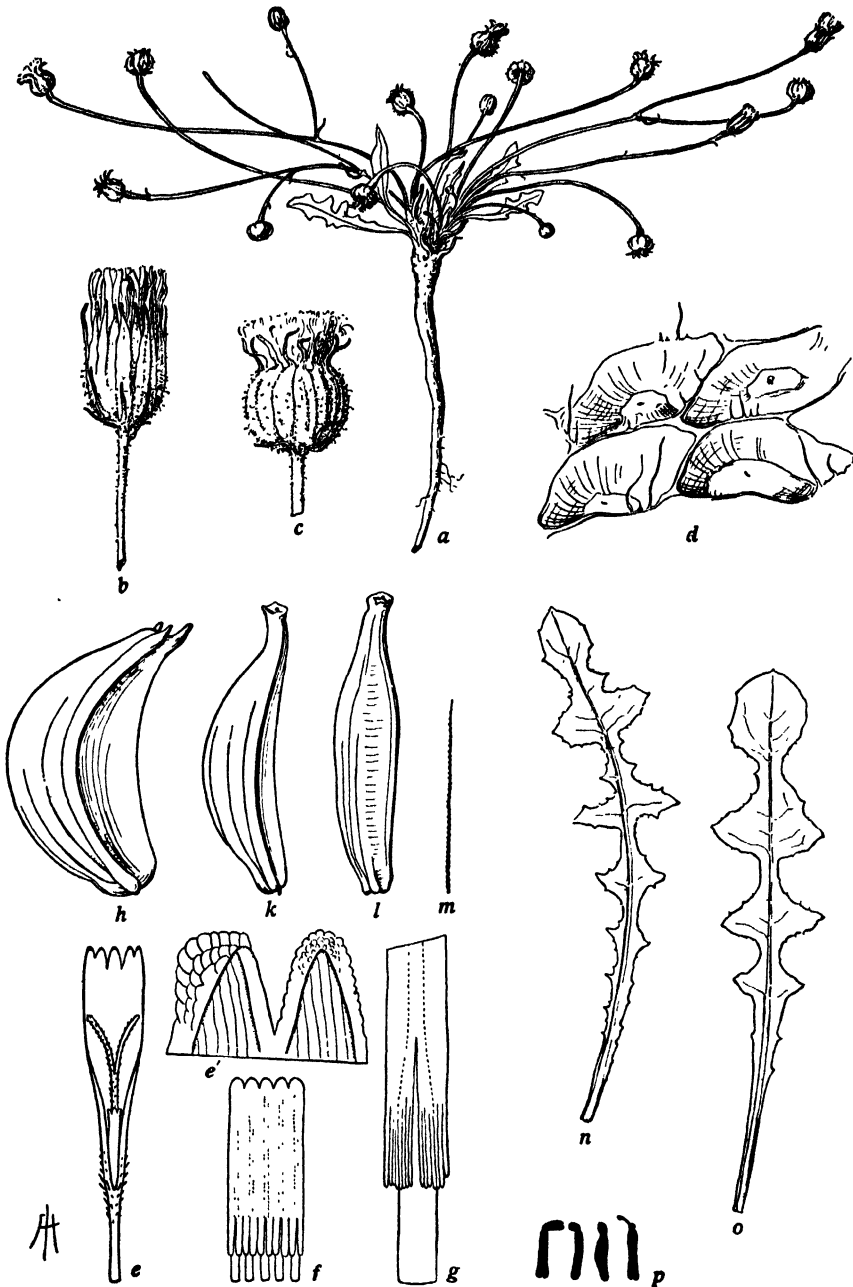


Fig. 244. *Crepis Dioscoridis argolica*, from type (UC 429365) and specimens descended from type: a, plant, $\times \frac{1}{2}$; b, flowering head, $\times 2$; c, fruiting head, $\times 2$; d, detail of receptacle, $\times 25$; e, floret lacking ovary, $\times 4$; e', detail of ligule teeth, $\times 32$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h-m, 3 achenes and a pappus seta, $\times 8$; n, o, leaves from a garden plant, $\times \frac{1}{2}$; p, somatic chromosomes, $n = 4$, $\times 1250$.

This subspecies is clearly more primitive than subsp. *typica*, especially in its less differentiated achenes. The type material was in an advanced stage when collected (June 28, 1930), and the only florets available were from late small heads. In cultivated progeny, however, the florets are as large as or larger than those of subsp. *typica*, whereas the anther appendages are broader and the style branches longer. Furthermore, from my limited observations, it seems probable that subsp. *argolica* behaves as a biennial under natural conditions. In all these features it shows definitely more resemblance to *C. patula* than to subsp. *typica* or the other two subspecies, and it may be considered the connecting link between *C. patula* and the rest of this section. It was observed in 1946 that greenhouse cultures of subspecies *argolica*, started at the same time as subsp. *typica* and *tirynthica*, produced flowers about 3 weeks earlier than either of those subspecies. Such precocity, if exhibited in the wild, would assist in preserving *argolica* as a distinct entity even if it came in contact with the other subspecies. Further study, therefore, may reveal sufficient grounds for recognizing this entity as a species. If it is actually local and ecologically isolated by adaptation to a strictly littoral environment, it must be a relic. Possibly it is in danger of early extinction.

157, c. *Crepis Dioscoridis tirynthica* Babc., Univ. Calif. Publ. Bot. 19: 400. 1941. Annual or biennial, about 3 dm high; root slender, woody; caudex simple, bearing one or several stems at summit; caudical leaves disappearing before flowers appear (in cult. up to 15 cm long, 3 cm wide, oblanceolate, lyrate pinnatifid with large ovate terminal segment, petiolate, denticulate, corneous-mucronate, sparsely pubescent with short pale glandless hairs); cauline leaves mostly linear, acuminate, acutely dentate, auriculate; stems several, elongated, decumbent or ascending, dichotomously branched, branches long, spreading, pedunculate or 1-5-furcate, arcuately ascending; peduncles 3-18 cm long, arcuate, glabrous or sparsely setulose; heads erect, medium, 50-70-flowered; involucre 9-12 mm long, 7-9 mm wide in fruit; canescent-tomentose, shortly setose; outer bracts 7-8 with 1-3 subtending, unequal, longest $\frac{1}{2}$ - $\frac{2}{3}$ as long as the inner, linear, smooth or setulose; inner bracts 12, lanceolate, gray with dark green dorsal stripe on upper half; receptacle areolate, glabrous; corolla 14 mm long; ligule 1.5 mm wide, yellow, paler on outer face; teeth 0.2-0.4 mm long; corolla tube 4 mm long, beset with minute (up to 0.08 mm) stout papilliform trichomes, sometimes with a few short stout several-celled hairs near base of ligule; anther tube 4×1.25 mm.; appendages 0.5 mm long, oblong, obtuse or acute; filaments 0.4 mm longer; style branches 2 mm long, 0.15 mm wide; achenes 3.5-4.5 mm long, marginal greenish-yellow, 1.5-2 mm wide, dorsally convex, 4-5-ribbed, ribs rounded, smooth, with 1 broad thin median ventral and two rounded lateral wings, contracted to the narrow apex, ribs and alae calloused at base, inner greenish-yellow, dorsally convex, strongly 4-5-ribbed, ribs rounded, smooth, ventrally straight with narrow median wing or \pm flattened, abruptly contracted at the narrow summit or contracted into a very short coarse beak, ribs swollen at base, forming a V-shaped callus; pappus little extruded, shorter than bracts, 3-4 mm long, deciduous. Flowering May. Chromosomes, $2n = 8$. See fig. 245.

Crepis Dioscoridis tirynica Babc., Univ. Calif. Publ. Bot. 19: 400. 1941, nomen perperam scriptum.

Known only from the type locality.

Greece: Argolis, Tiryns, St. Elias monastery, *Costopulos* in 1931 (UC 446468) type; ex hort. genet. Calif. (UC) progeny of type.

This subspecies is closest to subsp. *argolica*, from which it differs in numerous characters, notably in the lyrate basal leaves, the more upright habit with narrower branching angles, the setose involucre with slightly longer bracts which remain

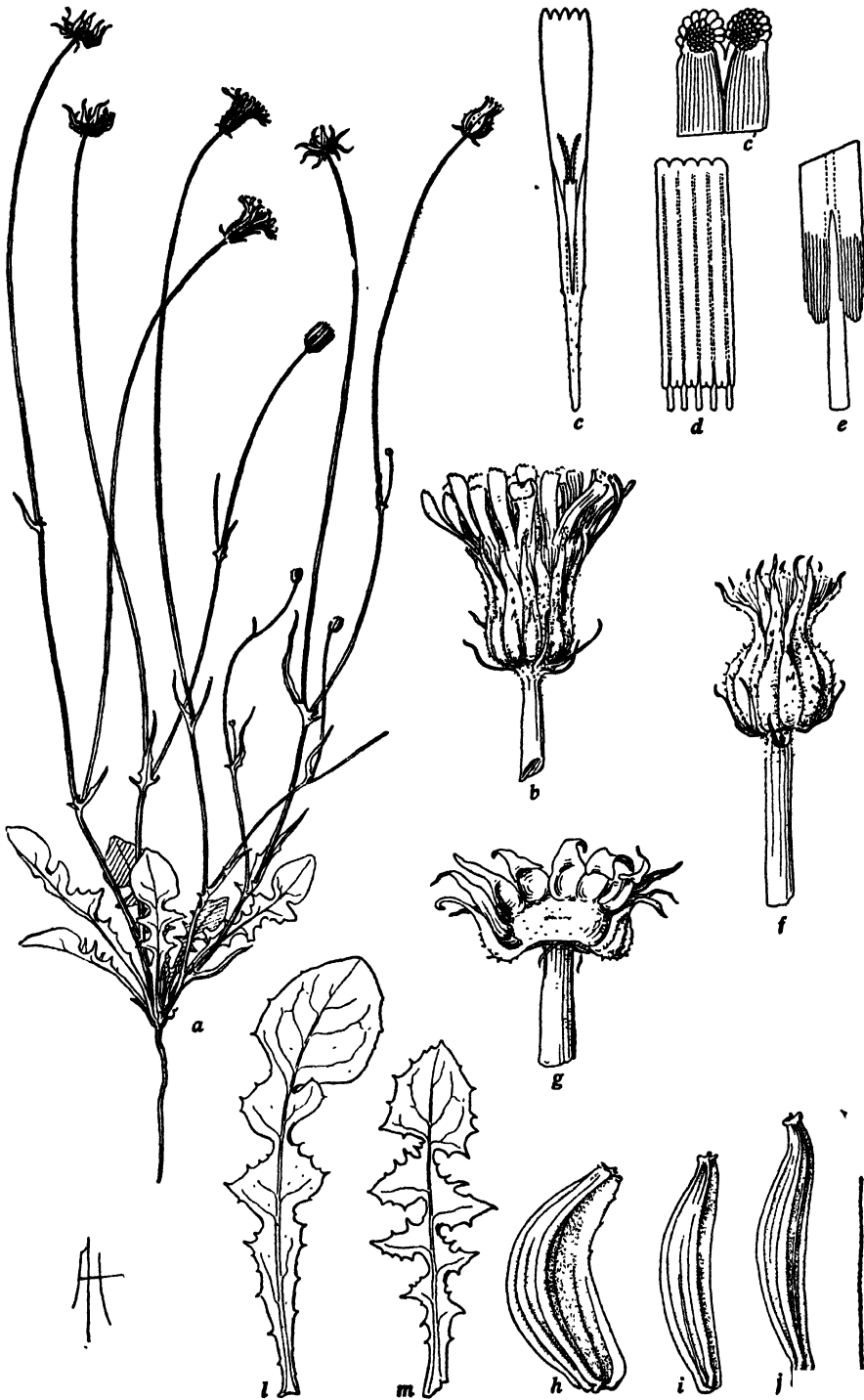


Fig. 245. *Crepis Dioscoridis tyrnithica*, from type (UC 446468) and specimens grown from seeds taken from the type: a, plant (type), $\times \frac{1}{2}$; b, flowering head, $\times 2$; c, floret lacking ovary, $\times 4$; d, detail of ligule teeth, $\times 50$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, fruiting head, $\times 2$; h-k, marginal and 2 inner achenes and a pappus seta, $\times 8$; l, m, caudal leaves, $\times \frac{1}{2}$.

nearly erect and exceed the pappus before becoming partly reflexed, the smaller florets with self-colored ligules (no red on outer face), the areolate receptacle, the marginal achenes yellow without small spines at the summit, and the inner achenes strongly ribbed with a V-shaped basal callus. In most respects subsp. *tiryntica* may be considered a more advanced subspecies than *argolica* and nearly as advanced as subsp. *typica*. But subsp. *tiryntica* shows more resemblance to subsp. *tubaeformis* and it may have been the progenitor of the latter.

The type locality of subsp. *tiryntica* is only a few kilometers distant from the type locality of subsp. *argolica*. It is rather remarkable that two such distinct forms should each be known only from a single locality in a region of comparatively easy access to collectors. This may be explained, perhaps, by their low stature, especially that of subsp. *argolica*, but it remains an interesting question whether the two are extremely local relics or whether they have a considerable distribution. It might seem highly probable that the two come into contact and hybridize, but it is possible that they are both ecologically and physiologically isolated, since subsp. *argolica* is known to be tolerant of the severe conditions existing on a gravelly strand near the sea and that it blooms earlier than subsp. *typica*. Nothing definite is known about the ecology of subsp. *tiryntica* except that it grows in association with subsp. *typica*. Further collections and field studies of these interesting forms are much to be desired.

157, d. ***Crepis Dioscoridis tubaeformis*** (Hal.) Babc., Univ. Calif. Publ. Bot. 19: 400. 1941. Annual, about 30 cm high, glabrous; root slender; caudex simple, bearing several stems at summit; caudical leaves 4–5 cm long, narrow, lanceolate, acute, pinnate, the lobes acute, narrowed into a short winged petiole; cauline leaves lanceolate to linear, acuminate, denticulate, sessile, acutely auriculate, laciniolate or uppermost entire; stems decumbent at base, strictly ascending, slender, simple and 1-headed or 1-furcate near base and 2-headed; peduncles 10–25 cm long, slender below, gradually thickened upward, twice as wide at summit, fistulose; heads small, containing about 25 fruits; involucre 8 mm long, 5 mm wide in fruit; outer bracts 10, $\frac{1}{3}$ as long as the inner; inner bracts 10–14; receptacle areolate; (no flowers on the type specimen); achenes all pale yellow, 4 mm long, incurved, constricted below the summit into a short coarse beak, dorsally convex, 8–10-ribbed, ribs rounded, smooth, ventrally concave with 3 strong ribs *but not alate*, marginal about 1 mm wide, firmly enclosed in the bracts and *with a long oblique basal scar*, inner with a 5–6-angled basal callosity; pappus about 1 mm long, not extruded, extremely fine, caducous. Flowering May; flowers not seen, probably yellow (see variants described below). Chromosomes, the $2n$ number is presumably 8, because, in forms similar to those described below, the karyotype corresponds to that of subsp. *typica*. See figs. 246, 247.

Crepis tubaeformis Hal., Conspect. Fl. Graec. 2: 230. 1902.

Known only from the type locality.

Greece: Aetolia, Mt. Taphiassos (now Klokova), on the shoulder toward Patras, 50–80 m alt., *Halacsy* 93/27 (UWG) type.

The two plants in the type collection are mounted on one sheet which bears the following annotation, evidently made by Halacsy (translated): "I took the plant to be *C. Dioscoridis* and gathered only these two specimens. They grew among loose rocks close to the middle of the slope called 'Kakiskala,' opposite Patras, on which stands *Teucrium Kalaeryanum*. In the immediate vicinity grew also *C. Dioscoridis*." The last sentence evidently refers to a population represented by his other collection of two plants (93/26) which he determined as *C. Dioscoridis*, but which appear to be

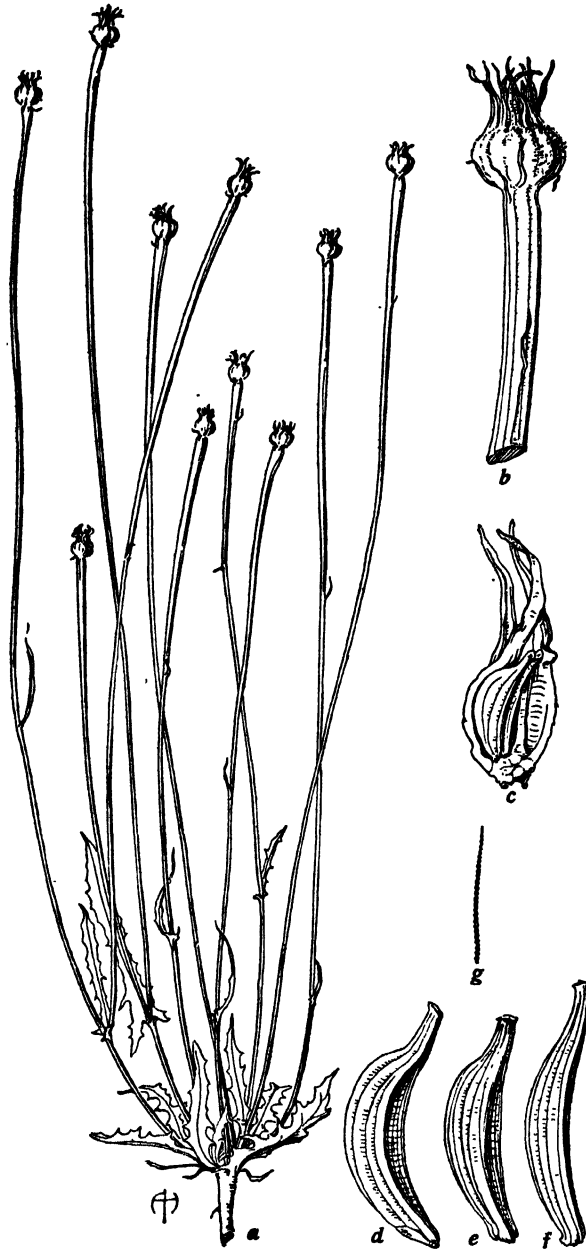


Fig. 246. *Crepis Dioscoridis tubaeformis*, from type (UWG): a, plant, $\times \frac{1}{2}$; b, fruiting head, $\times 2$; c, 3 outer involucral bracts, 2 marginal achenes, and part of receptacle, $\times 4$; d-g, a marginal achene, 2 inner ones, and a pappus seta, $\times 8$.

intermediate forms produced by natural hybridization between subsp. *tubaeformis* and subsp. *typica*. They are described below as m.v. 1.

In 1931 Professor P. Th. Anagnostopoulos, Director of the Horticultural Experiment Station in Athens, kindly sent his assistant, Mr. Setta, to the type locality for specimens and seeds. Among the specimens received were several forms differing in various combinations and degrees of expression of certain characters. One of these corresponded to Halacsy's no. 93/26; three others are listed as m.v. 2, 3, 4. As stated above, about one hundred progeny were grown at Berkeley in 1932 from seeds collected by Setta, and these exhibited great variability, ranging from *tubaeformis*-like to *typica*-like plants. Because Setta's collections contained no specimens of typical subsp. *tubaeformis*, it might be conjectured that since the year 1893 this subspecies, at least in that locality, has been wiped out by the hybrid progeny. But further field observations in Aetolia are needed to establish this assumption.

Minor Variants of *C. Dioscoridis tubaeformis*

1. ($\times C. dioscoridis tubaeformis \times typica$.) Annual, 3–3.5 dm high; caudical leaves up to 15 cm long, oblanceolate, denticulate or pinnate, petiolate; lower cauline leaves similar or sessile, middle and upper ones linear, acuminate, acutely auriculate; stem erect, 4–5-furcate from base upwards; peduncles 1.5–13.5 cm long, slender below, gradually thickened toward base of head, fistulose; heads small, erect, about 25-flowered; involucre cylindric in anthesis, becoming globose, 5–6 mm wide in fruit; corolla 11 mm long; ligule 1.4 mm wide; teeth 0.4–0.6 mm long; corolla tube 2.5 mm long, sparsely pubescent with acicular hairs up to 0.2 mm long; anther tube 3.3×1 mm dia.; appendages 0.5 mm long, obtuse; filaments 0.5 mm longer; style branches 1.5 mm long, 0.1 mm wide, yellow; achenes 4 mm long, all brownish-yellow, strongly incurved, 8–10-ribbed, ventrally concave with 3 strong ribs, middle rib subulate, dorsally convex with obscure basal scar; inner achenes with a 5-angled basal callus; pappus 2–3 mm long, very fine, white, caducous. *Halacsy 93/26* (UWG), at the type locality for *C. tubaeformis*; *Setta* in 1931 (UC), same locality.

2. ($\times C. dioscoridis tubaeformis \times typica$.) Resembles m.v. 1 in habit and mature heads; leaves and florets lacking; involucre 5–6 mm wide in fruit; achenes similar to those of m.v. 1, but inner achenes faintly rugulose and of two colors, some yellowish, the others dark brown, like those of *C. Dioscoridis typica*. *Setta* in 1931 (UC), type locality for *C. tubaeformis*.

3. ($\times C. dioscoridis tubaeformis \times typica$.) Resembles m.v. 1 in habit and mature heads; florets lacking; involucre 5–6 mm wide in fruit; achenes like those in m.v. 2, except that all the fertile inner achenes are dark brown and spiculate, like those of *C. Dioscoridis typica*. *Setta* in 1931 (UC), type locality for *C. tubaeformis*.

4. ($\times C. dioscoridis tubaeformis \times typica$.) Resembles m.v. 1 in habit, but very robust and up to 5 (†) dm high; mature heads larger; involucre 6–7 mm wide; inner achenes all dark brown, spiculate. *Setta* in 1931 (UC), type locality for *C. tubaeformis*.

Relationship

Crepis Dioscoridis, considered in the broad sense of the present treatment, is not merely a polymorphic species in the ordinary meaning of that term. It is clear that there have been included here a series of morphologically distinct forms which differ in respect to many genetic factors but which are still so similar in genetic constitution that they hybridize freely and produce highly fertile hybrids. Yet they all occur in the same geographic area and there is no definite proof that any of them is ecologically isolated from the others, although subsp. *argolica* may be so isolated, and it is known to bloom earlier than the other subspecies. Under these conditions, the present treatment is, in my opinion, the fairest representation of the true state of things in nature. But, to complete the picture, it should be emphasized that these subspecies can be arranged in a phyletic series on the basis of comparative morphology. The most primitive is subsp. *argolica*, and it shows most resemblance to *C. patula*. From subsp. *argolica*, or the stock it represents, 2 lines arose. One includes *C. Dioscoridis typica* and the much more advanced *C. multiflora* (q.v.). The other includes *C. Dioscoridis tirynthica* and *C. Dioscoridis tubaeformis*; and the highly specialized *C. Zacintha* also appears to have arisen from this line.

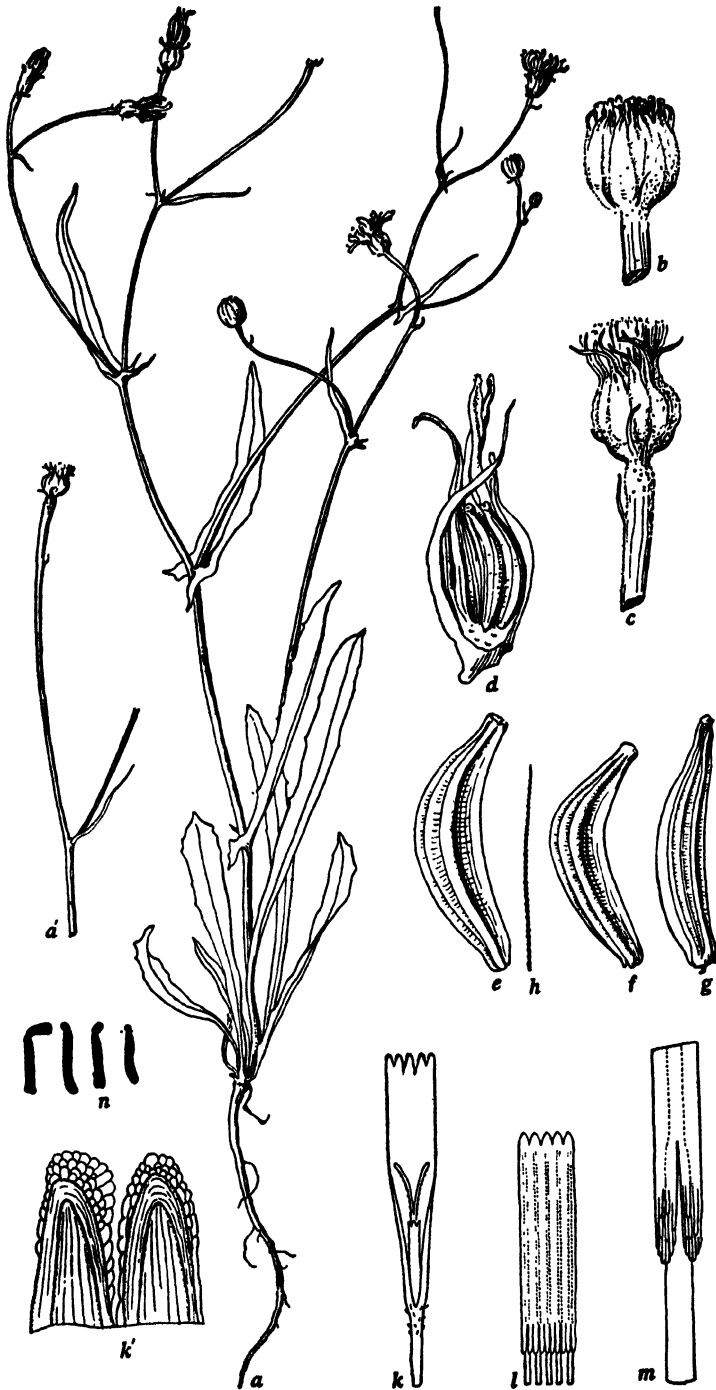


Fig. 247. *Crepis Dioscoridis tubaeformis*, a-m, from Halacsy in 1893 (UWG 93/26); n, from minor variant ex hort. genet. Calif. 32.3069 (grown from seeds received from the type locality through Dr. P. Anagnostopoulos): a, plant, $\times \frac{1}{2}$; a', branch, peduncle, and head, $\times \frac{1}{2}$; b, c, flowering and fruiting heads, $\times 2$; d, part of a mature head showing inner bracts, 2 marginal achenes, and part of receptacle, $\times 4$; e-h, marginal achene, 2 inner achenes, and a pappus seta, $\times 8$; k, floret lacking ovary, $\times 4$; k', detail of ligule teeth, $\times 32$; l, anther tube, $\times 8$; m, detail of appendages, $\times 32$; n, somatic chromosomes, $n = 4$, $\times 1250$.

158. *Crepis multiflora* Sibth. et Sm.

Fl. Graec. Prod. 2: 138. 1813; Fl. Graec. 9: t. 806. 1837. (Fig. 248.)

Annual, 0.7–3.5 dm high; caudical leaves few, 1–5 cm long, 0.5–1 cm wide, oblanceolate, obtuse, dentate or runcinate-pinnatifid, corneous-mucronate, attenuate into a short winged petiole with broader base, glabrous on both sides; lower cauline leaves sessile, amplexicaul, acutely auriculate, upper cauline leaves lanceolate or linear, acute, entire, auriculate; stem upright, dichotomously branched from near base, with a few weak or nearly equal divaricate secondary stems, the aggregate inflorescence cymosely many-headed, stem, branches, and peduncles terete, striate, \pm gland-puberulent or glabrous, the peduncles slender, not thickened near head; heads erect, small, 30–65-flowered; involucre cylindric-campanulate, becoming ovoid in fruit, 8–9 mm high, 5 mm wide at receptacle, becoming pale spongy-thickened at base; outer bracts 8–12, very narrow, subulate, about $\frac{1}{3}$ as long as inner bracts, glabrous; inner bracts 8–13, lanceolate, acute, scarious-margined, ventrally glabrous, dorsally glandular-setaceous with short yellowish bristles, navicular and strongly carinate in fruit, partly enclosing marginal achenes; receptacle areolate-fimbriate, areolae 0.4–0.6 mm wide, glabrous, conically elevated, fimbriae low, not ciliate; corolla about 7.5 mm long; ligule 1.3 mm wide, teeth 0.25–0.5 mm long; corolla tube about 2.75 mm long, slender, sparsely beset above with minute trichomes or glabrous; anther tube about 2.5×0.75 mm; appendages 0.5 mm long, obtuse; filaments very short; style branches about 1.5 mm long, slender, yellow; achenes biform, or the typical marginal achenes absent; marginal achenes 3.5–4 mm long, more attenuate toward summit than toward base, with or without expanded pappus disk, ventrally concave, pale, smooth, unequally ribbed, the median and lateral ribs stronger, dorsally convex, dark brown, 5-ribbed, ribs equal, narrow, rugulose, strongly calloused, and with a small dorsal scar at base; inner achenes 3–3.5 mm long, dark brown, curved or straight, fusiform, strongly attenuate below the narrow (0.15 mm wide) summit, with slightly expanded paler pappus disk, less attenuate to the narrow calloused base, 10-ribbed, ribs very narrow, pale, rugulose or finely spiculate near summit, interspaces dark; pappus about 3.5 mm long, white, fine, soft, \pm united at base, caducous. Flowering April–June; flowers yellow. Chromosomes, $2n = 8$.

Endoptera dichotoma Boiss. et Bal., Diagn., ser. 2, 3: 98. 1856.*Crepis dichotoma* Boiss. et Bal., op. cit., 99.*Hieraciodes multiflorum* O. Kuntze, Gen. 1: 346. 1891.

E. Greece, Aegean Archipelago, Crete, Scarpanto, Rhodes, and W. Asia Minor. The type locality, "in campis Thraciae," is dubious.

Greece: without definite locality, ex *J. Sibthorp* (Oxford-Druce, authentic specimen); Attica, *Heldreich* in 1877 (Genoa); Attica, Laurium, *Heldreich* in 1885 (RB, UC) m.v. 1; Attica, Rapti, *Guil* in 1929 (UC). **Aegean Archipelago:** Cyclades, Mikra Kamini I., near Thera I., *Halacsy* in 1911 (UWH) m.v. 1; Cyclades, Kythnos I., *Heldreich* in 1890 (UWH); *ibid.*, in 1892 (Ms); Cyclades, Tenos I., *Heldreich* in 1901 (UWH); Cyclades, Syra I., *Aucher-Eloy 3843* (DC) m.v. 1. **Scarpanto** (Karpethos): Pigadia, *Pichler 422* (BB) m.v. 2; *ibid.*, Olympus, *Forsyth Major 32* (RB) m.v. 2. **Asia Minor:** Smyrna, shady embankments along roads, very rare, *Balansa 254* (Bo, Genoa) m.v. 2; Tapasby, near Lugia-Hamam, on seashore, *Sintenis 981* (B, BM) m.v. 3.

Minor Variants of C. multiflora

1. The typical marginal achenes absent. *Heldreich* in 1885 (RB), region of Laurium, Attica; *Halacsy* in 1911 (UWH), Mikra Kamini I., Cyclades; *Aucher-Eloy 3843* (DC), Syra I., Cyclades.

2. (*Endoptera dichotoma* Boiss. et Bal., Diagn., ser. 2, 3: 98. 1856; *Crepis dichotoma* Boiss. et Bal., op. cit., 99.) With fewer and stouter branches and peduncles and hence more conspicuously dichotomous; typical marginal achenes lacking. *Balansa 254* (Bo, Genoa), rare along roads

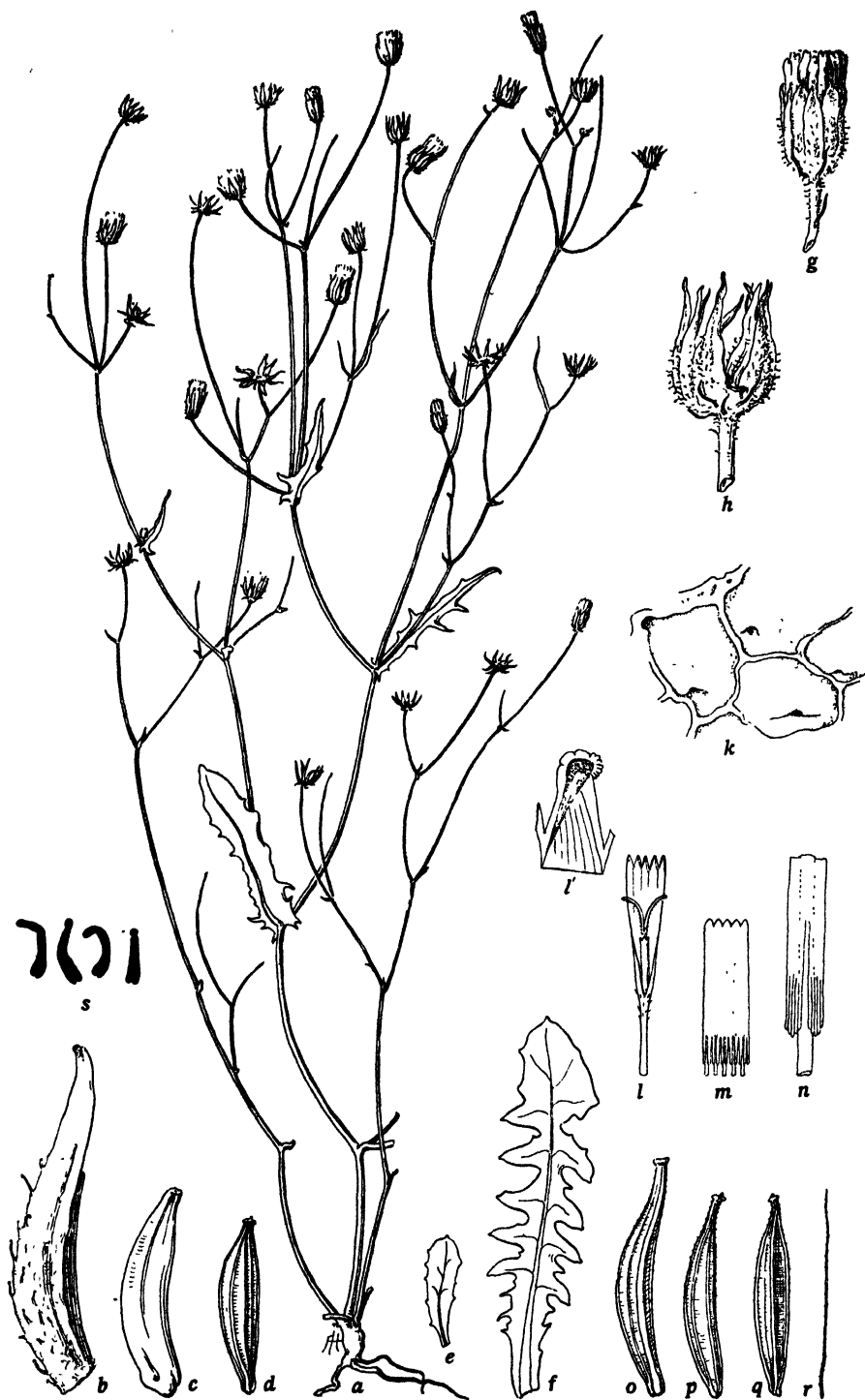


Fig. 248. *Crepis multiflora*, a-d, from authentic specimen (Oxford, herb. G. C. Druce); e-r, from *Sintenis* 931 (B); s, from hort. genet. Calif. 3062 (grown from seeds collected in Attica, Greece, by Miss S. P. Topali; cf. UC 463906, 519496): a, plant lacking lower leaves, $\times \frac{1}{2}$; b, marginal achene partly enclosed by bract, c, marginal achene and, d, inner achene, $\times 8$; e, f, caudical leaves, $\times 1$; g, h, young and old heads, $\times 2$; i, detail of receptacle, $\times 25$; j, floret lacking ovary, $\times 4$; k, detail of ligule tooth, $\times 25$; l, m, anther tube, $\times 8$; n, detail of appendages, $\times 32$; o-r, a marginal, 2 inner achenes, and a pappus seta, $\times 8$; s, somatic chromosomes, $n=4$, $\times 1250$.

around Smyrna; *Pichler 422* (BB), Pigadia, Scarpanto (Karpathos); *Forsyth-Major 32* (BB), Olympus, Scarpanto (Karpathos).

3. Secondary stems from base of plant equal or nearly equal to the primary stem, thus producing a rather low divaricate plant of quite distinct habit from the typical form; achenes biformic; marginal achenes more slender than in typical form and more attenuate at summit with expanded pappus disk; inner achenes so strongly attenuate as to be short-beaked, alternate ribs very faint, sometimes absent. *Sintenis 981* (B, BM), on seashore near Lugia-Hamam, Asia Minor.

Relationship

Crepis multiflora is nearest to *C. Dioscoridis typica*, from which it is very distinct in size and form of involucre, size of corolla and anther tube, size and form of achenes, and habit of plant. It is, however, much more similar to *C. Dioscoridis* in habit, flowers, and fruits than is *C. Zacintha*. Experiments have shown that it is fairly close genetically to *C. Dioscoridis*, although it is less close than are the four subspecies of *C. Dioscoridis* to one another. Two hybrids from the cross, *C. multiflora* × *C. Dioscoridis typica*, produced, respectively, 14 per cent and 33 per cent of fertile achenes after open-pollination; and 2 hybrids from the cross, *C. multiflora* × *C. Dioscoridis tubaeformis*, produced 0 per cent and 7 per cent of fertile achenes. Such low hybrid fertility, considered along with the geographic isolation of *C. multiflora*, fully justifies its status as a species. Next to *C. Zacintha*, *C. multiflora* is the most advanced species of this section on the basis of reduction in size of plant, heads, florets, and achenes; and it is the most precocious species of this section.

159. *Crepis Zacintha* (L.) Babc.

Univ. Calif. Publ. Bot. 19: 404. 1941. (Fig. 249.)

Annual, 2–3 dm high; root slender; caudex short, swollen, leafy in rosette stage; caudical leaves disappearing early, up to 20 cm long, 4 cm wide, lyrate-pinnatifid, terminal segment large, ovate or truncate, obtuse, lateral segments remote, triangular, acute, corneous-mucronate, sometimes dentate, pubescent with short pale glandless hairs; lower cauline leaves similar, middle ones lanceolate, acuminate, sessile, acutely auriculate, uppermost bractlike; stem erect, simple in reduced specimens, branched above or from near base, or with 1 or 2 secondary stems, terete, striate, pubescent below with short glandless hairs, glabrous above, branching habit dichotomously cymose with some heads sessile at or near bifurcations, other heads pedunculate; peduncles 1–3 cm long, rather stout, fistulose, glabrous; heads small, about 30-flowered; involucre before anthesis cylindric; outer bracts 5, lanceolate, unequal, longest $\frac{1}{2}$ as long as inner ones, glabrous or tomentulose at base; inner bracts 10, lanceolate, obtuse, ciliate at tip, tomentulose at base, ventrally pubescent with very short shining hairs, not enclosing marginal ovules, in and after anthesis lower half of each inner bract becoming greatly swollen, strongly angular with upper half nearly horizontal, concealing pappus, indurate, completely enclosing achene, \pm fused with its pericarp; receptacle areolate, naked; corolla 7 mm long; ligule 1.25 mm wide, yellow, deep purplish-red on outer face; teeth 0.2–0.4 mm long, purple-crested; corolla tube 1.4 mm long, pubescent with 2-celled acicular hairs up to 0.3 mm long; anther tube 2.4×1 mm dis.; appendages 0.4 mm long, lanceolate, acuminate; filaments 0.4 mm longer; style branches 1 mm long, 0.1 mm wide, green; achenes biform; marginal achenes 2–2.5 mm long, laterally strongly compressed, triangular, base pointed, summit truncate or rounded, strongly constricted below the pappus disk, which is bent at a right angle in a ventral direction, ventrally flat, and pubescent with very short white hairs; inner achenes about 2.5 mm long, yellowish, obconic, somewhat compressed laterally, constricted below the narrow pappus disk, attenuate to the narrow calloused base, 10-ribbed, ribs



Fig. 249. *Crepis Zacintha*, a-o, from Babcock 349 (UC 429427); p, from hort. genet. Calif. 3439 (grown from seeds received from Paris Bot. Gard.): a, plant, $\times \frac{1}{4}$; b, young flower heads, $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule teeth, $\times 50$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, fruiting head, $\times 2$; g, fruiting head, longitudinal section, $\times 2$; h-j, inner involucre bracts from 3 heads of different ages, $\times 4$; k, mature bract enclosing marginal achene, $\times 8$; l, m, marginal and adjacent inner achenes, $\times 8$; n, o, another marginal and a typical inner achene, $\times 8$; p, somatic chromosomes, $n = 3$, $\times 1250$.

rounded, smooth; pappus white, about 1.5 mm long, fine, soft, strongly and closely barbellulate, caducous. Flowering June. Chromosomes, $2n = 6$.

Lapsana Zacintha L., Sp. Pl. 2: 811. 1753.

Rhagadiolus Zacintha Desf., Fl. Pedem. 1: 227. 1785.

Zacintha verrucosa Gaertn., Fruct. 2: 358. 1791.

Mediterranean reg., fields and wastes up to 600 m alt.

This species occurs in all parts of the Balkan Pen. as far north as Bulgaria acc.

to Markgraf (805). It is reported to occur in Syria and N. Africa by Velenovsky (355), but no specimens from those regions have been seen by me.

Although somewhat variable in shape of leaves and time of flowering, as indicated by two cultivated strains (hort. genet. Calif. 2909, 3439), this is such a distinct species that it was not considered necessary to examine and cite numerous specimens.

Monomorphic, so far as known to me.

Greece: Thessaly, below Kastanea, toward Kalabaka, grassy slopes among oaks, *Babcock 349* (UC). **Serbia:** Crovenie (= Croveni-Breg ?), *Mougeot* in 1833 (NY). **Hercegovina:** Hostar, Narenta Ufer, dry fields, *Halacsy 92* (US); Trebinje, Kloster Duze, *Baenitz* in 1898 (US). **Italy:** Istria (NY); Modena, Villa Cassinalbo, in 1883 (US). **France:** Var. Antibes, *Bourgeau* in 1861 (US); Herault, between the Aresqiers and the Salins de Frontignan, *Mandon* in 1890 (US); near Marseille, *Roux 2728* (US). **Turkey:** Bithynia, near Seutari, *Krause 3205* (UC); Cilicia, *Peronin* (UC).

Relationship

Although this species was retained as a genus by Hoffmann (E. and P. 360), it is placed between *Arnoseris* and *Rhagadiolus*; but it is not closely related to either of these genera. Its close affinity with *C. Dioscoridis*, however, was recognized by Cassin (Dict. 25: 62. 1822), who placed the two genera *Gatyona* and *Zacintha* close to each other, except that they were separated by *Nemauchenes* because of the superficial similarity of *C. Zacintha* to *C. aspera*.

Morphological evidence of the close relationship between *C. Zacintha* and the other species of sec. 23 is clear and convincing, especially the closed, indurate involucre in fruiting heads, which is unique in this section (see Part I, p. 46). Its specialized involucre and consequently modified achenes, together with its very low chromosome number, annual habit, and wide distribution, all mark it as a very advanced species. Yet it must have been derived from a primitive type which probably resembled *C. patula*. Its present distribution, especially its occurrence in all parts of the Balkan Pen., is in good agreement with the assumption that the progenitor(s) of this section migrated from the east through the Balkan Pen. to N. Tunis and E. Algeria. From the Balkan region *C. Zacintha* has spread both westward and eastward.

SECTION 24. PHYTODESIA

The 10 species in this section are all either annual or monocarpic plants. *C. nicaeënsis* is the only one that behaves characteristically as a biennial, and even in this species occasional plants will produce flowers and fruits during the first growing season after germination. In all these species the plant is always more or less pubescent and either erect and \pm branched or low and bushy in habit. The leaves are usually oblanceolate and pinnatifid; and the heads are medium to small or very small, with the outer bracts of the involucre much reduced. The achenes are always small, 10-ribbed or -striate, and either unbeaked or beaked. The pappus is short, white, fine or very fine, and 1-2-seriate. In short, this is a group of rather similar advanced species; yet they exhibit a considerable range in degree of advancement. They fall into 4 subgroups, with one species, *C. insignis*, a connecting species between two of the subgroups. The 4 subgroups are: (1) *C. nicaeënsis*; (2) *C. capillaris* and *C. parviflora*; (3) *C. neglecta*, *C. corymbosa*, *C. fuliginosa*, and *C. cretica*; (4) *C. apula* and *C. Suffreniana*.

(1) *C. nicaeënsis* is a bridging species between this section and sec. 10, since it is obviously related to *C. biennis* on morphological grounds. Although it has only 4 pairs of chromosomes, it could have been derived from the same 5-paired line as *C. biennis*.

(2) *C. capillaris* with 3 pairs of chromosomes and *C. parviflora* with 4 pairs are closely similar morphologically and it is probable that they were derived from the same ancestor. To *C. neglecta* these species exhibit less marked resemblances; and the chromosomes of *C. capillaris* are more like those of *C. parviflora* than *C. neglecta*.

Although *C. insignis* is known only from the type specimen, it is so distinct from the other species of this section that its recognition as a species seemed to be warranted. Unfortunately, mature achenes are not available, but from the immature ones it seems probable that the mature ones are definitely attenuate and more like those of *C. neglecta* than *C. parviflora*. The involucre in *C. insignis*, however, is more like that of *C. parviflora*; and its one known station is centrally located in the distribution area of *C. parviflora*. For the present, therefore, this species may be considered as a connecting species between subgroups (2) and (3) of this section.

(3) *C. neglecta*, *C. corymbosa*, and *C. cretica* all have 4 pairs of chromosomes, whereas *C. fuliginosa* has only 3 pairs. In all 4 species the chromosomes are somewhat narrower than those of most *Crepis* species, and it was discovered by Tobgy that this peculiarity is more extreme in *C. fuliginosa* than in *C. neglecta*. *C. neglecta* has long been troublesome to those who would draw a sharp line between "Eucrepis" and "Barkhausia," i.e., between the species of this genus having unbeaked and beaked achenes; this is because the achenes of *C. neglecta* are sometimes shortly beaked. Morphologically, *C. neglecta* is actually so close to these other three species that they have been treated as one inclusive species by some taxonomists. However, the morphological differences between them, though small, are fairly constant; and the 4 entities are isolated, either geographically or genetically, from one another almost completely. The cytogenetic evidence discovered by Tobgy, that *C. fuliginosa* either originated directly from *C. neglecta* or that the two originated from a common ancestor, provides a sound foundation not only for the present classification of these species, but also for one of our hypotheses concerning the basic genetic processes involved in the evolution of *Crepis* (see Part I, pp. 145, 148).

(4) *C. apula* and *C. Suffreniana* are the most reduced species in this section, at least in some parts of the plant, but especially in the florets and flower parts. In fact, *C. Suffreniana*, at least in its flower parts and in the size of its chromosomes, must be recognized as the most reduced species in the genus. Although these two

species are certainly related to the *C. neglecta* subgroup, they differ in several ways, most notably in their dark-colored achenes and in their distinct karyotypes. Probably they were derived from an ancestor which was closely related to *C. neglecta* or to its progenitor.

The geographic distribution of this section (fig. 250) is very interesting. In its indigenous distribution, *C. nicaeensis*, the most primitive member, is apparently

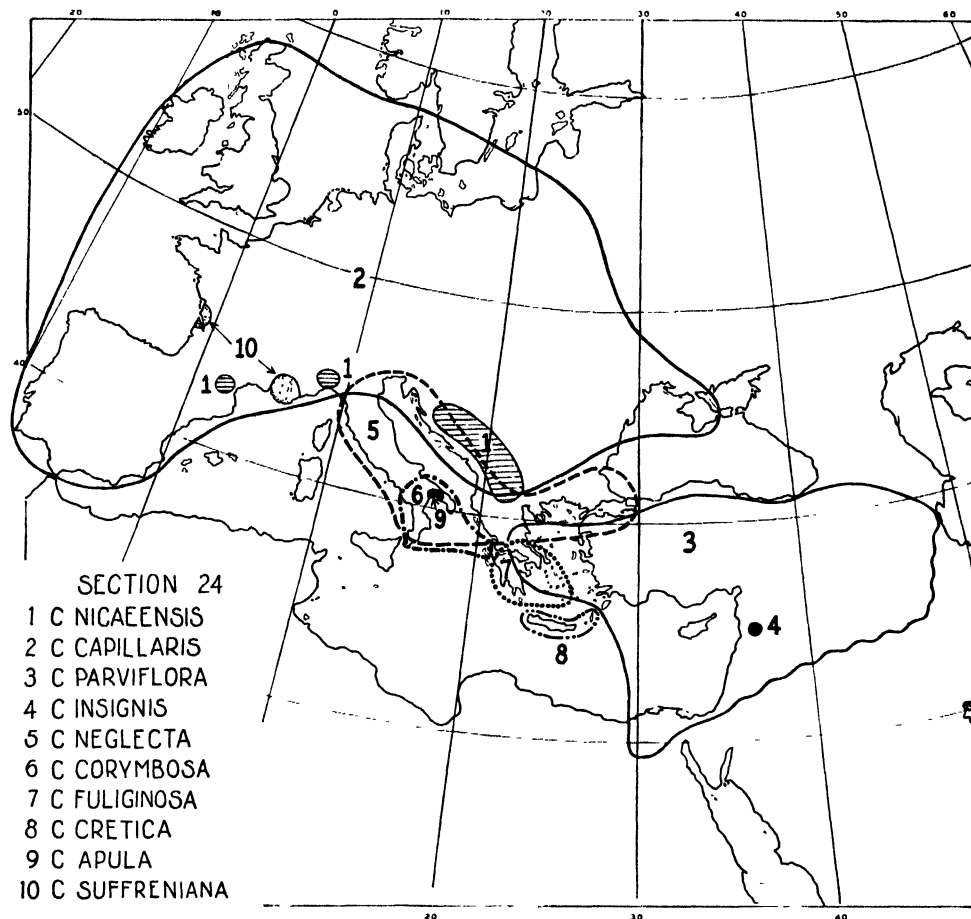


Fig. 250. Geographic distribution of the 10 species in sec. 24. *C. insignis* is known from a single station, shown as a solid circle. *C. apula* is known only from the vicinity of Taranto, Italy. Based on Goode Base Map No. 124. By permission of the University of Chicago Press.

restricted to the Dalmatian and adjacent mountains, the Maritime Alps, and the S.E. Pyrenees. But, as a hayfield weed, it has become widely distributed in Europe and even in other continents. The next two species, *C. capillaris* and *C. parviflora*, are both widely distributed species, the former in most of Europe, and the latter from E. Greece to the Caucasus, Iraq, and Egypt. *C. capillaris* is a "plastic" species in its environmental adaptations, but is generally better suited by a more humid climate, whereas *C. parviflora* is definitely adapted to more xerophytic conditions. The *C. neglecta* group of four species, although more advanced, are restricted to the N. Mediterranean littoral from Italy to the Aegean, Crete, and N.W. Asia Minor, the other species of this subgroup occupying small areas in this general region. Furthermore, *C. apula* and *C. Suffreniana* are very local maritime species, one find-

ing habitat in Italy, the other in France. Thus, the six most advanced species are restricted in distribution and five are narrow or local endemics. Apparently, in these species, specialization has accompanied physiological adaptation to local environmental conditions. Geographic isolation, however, has certainly been important to the insular species, *C. cretica*; and it may have played an important role in the evolution of the other advanced species also. Finally, *C. insignis*, the connecting species between *C. parviflora* and the *C. neglecta* subgroup, is known as yet only from one station in Syria. The distributional picture of the section, as a whole, fits beautifully into the general hypothesis that *Crepis* had its origin somewhere to the east of the Mediterranean reg. and that certain more primitive species migrated into the mountains of the Mediterranean reg. and gave rise to more advanced descendants, some of which became widespread and others restricted according to the circumstances under which they developed.

Key to the Species of Section 24

Achenes never or very rarely beaked; heads erect before anthesis.

Outer involucre bracts 7–9, the longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner; inner bracts 8–16, mostly 10–15; anther tube 3–4 mm long.

Involucres 8–10 mm long, campanulate in fruit; receptacle ciliate; achenes golden brown, 2.5–4 mm long. 160. *C. nicaeensis*, p. 766

Involucres 5–8 mm long, turbinate in fruit; receptacle glabrous; achenes pale or dark brown, 1.5–2.5 mm long. 161. *C. capillaris*, p. 769

Outer involucre bracts 5, about $\frac{1}{2}$ as long as the inner; inner bracts 8–9 or 10; anther tube 2–2.7 mm long.

Plant 1-stemmed, the stem erect, many-headed; caudical leaves with broad lateral lobes; style branches green; achenes not strongly constricted at the apex. 162. *C. parviflora*, p. 775

Plant many-stemmed, the stems 1–3-headed; caudical leaves with narrow lateral lobes; style branches yellow; achenes strongly constricted at the apex. 163. *C. insignis*, p. 778

Achenes, at least the inner, beaked, or if not definitely beaked (*C. neglecta*), then the heads nodding before anthesis.

Outer involucre bracts 4–6, very small; inner bracts 7–9, or if sometimes more than 9 (*C. neglecta*, *C. corymbosa*), then the achenes pale brown, 2–2.8 mm long.

Plant taller, 1-stemmed, the stem elongated, paniculately branched, or if plant sometimes low, with several short stems (*C. neglecta*), then the achenes not definitely beaked.

Stem hispidulous below, glabrescent above; involucres glabrous, tomentulose or gland-pubescent, or rarely with greenish setae near apex of the inner bracts; achenes gradually attenuate to the apex but scarcely beaked, the marginal not infolded and retained by the inner bracts. Italy to N. Greece, S. Bulgaria, Macedonia, Thrace, and N.W. Asia Minor. 164. *C. neglecta*, p. 780

Stem hispid with fine yellowish setae; involucres setose with yellow or greenish glandless setae or rarely glabrous; achenes, at least the inner, with a beak less than 1 mm long, the marginal infolded and often retained by the inner bracts. S. Italy, Corfu, and Cephalonia. 165. *C. corymbosa*, p. 783

Plant low, usually with several short stems; achenes definitely beaked.

Caudical leaves denticulate to pinnately parted with 4–6 pairs of lateral segments; achenes mostly broader and more coarsely beaked. S. Greece and E. Thessaly. 166. *C. fuliginosa*, p. 785

Caudical leaves dentate to pinnately parted with 6–10 pairs of lateral segments; achenes narrower, more delicate, and more finely beaked. Crete. 167. *C. cretica*, p. 789

Outer involucre bracts 10–12, larger, $\frac{1}{4}$ – $\frac{1}{2}$ as long as the inner; inner bracts 10–16; achenes nearly black or reddish-brown, 3–4 mm long.

Involucres pubescent with dark gland hairs; corolla 8–9 mm long; anther tube 2.5 mm long; achenes dark brown or black.....168. *C. apula*, p. 790

Involucres finely setulose with dark green glandless hairs; corolla 5 mm long; anther tube 1 mm long; achenes bright reddish-brown.....169. *C. Suffreniana*, p. 793

160. *Crepis nicaeënsis* Balb.

Ex. Pers., Syn. Pl. 2: 376. 1807; Mem. Acad. Sci. Turin, 16: 226. 1809. (Pl. 23. Fig. 251.)

Annual or biennial, 2.5–11 dm high; caudical leaves few or many, up to 19 cm long, 4 cm wide, usually much smaller, oblanceolate, obtuse, runcinate-pinnatifid, dentate or finely and remotely denticulate, attenuate into a short winged petiole with clasping base, \pm hispidulous with short yellow glandless hairs; lowest cauline leaves similar but with longer petioles; other cauline leaves mostly lanceolate, sessile, broad or narrow at base and usually with short or long acuminate pendent auricles; stem erect, terete, sulcate, densely hispidulous below, cymosely branched near summit or from the middle, the branches short and pedunculate or long and 2–6-headed, the aggregate inflorescence corymbiform; peduncles rather slender, slightly thickened near head, like involucre, \pm canescent-tomentose and \pm pubescent with long and short glandular or glandless hairs; heads erect, medium, less than 2 cm wide in anthesis, 50–60-flowered; involucre campanulate, 8–10 mm high, 4–6 mm wide at receptacle; outer bracts 7–9, linear, acute, $\frac{1}{3}$ – $\frac{1}{2}$ ($\frac{2}{3}$) as long as the inner, becoming lax; inner bracts 10–15, lanceolate, strongly attenuate, obtuse at the ciliate tip, ventrally glabrous or very rarely sparsely pubescent (see m.v. 6), dorsally becoming strongly carinate-indurate in fruit, partly enclosing marginal achenes, spongy-thickened at base when mature; receptacle convex, alveolate-fimbrillate, alveolae 0.5–0.6 mm wide, fimbrillae 0.1–0.2 mm high, finely ciliate; corolla 11 mm long; ligule 1.6 mm wide (1 mm at summit), teeth 0.25 mm long; corolla tube 3 mm long, slender, upper part of tube and lower part of ligule sparsely pubescent with several-celled trichomes up to 0.25 mm long; anther tube 3.8×1.4 mm dis.; appendages 0.8 mm long, lanceolate, acute; filaments 0.6 mm longer; style branches 1.7 mm long, slender, dark green, yellow on stigmatic surface; achenes golden brown, 2.5–3.8 mm long, about 0.6 mm wide, fusiform, the marginal curved, shortly attenuate to the narrow (0.3 mm wide) summit with pale erect pappus disk, similarly attenuate to the narrow faintly calloused base, 10-ribbed, ribs broad, rounded, smooth or faintly rugulose below and finely spiculate near the apex; pappus white, 4–5 mm long, 2-seriate, fine, soft, \pm united at base, deciduous. Flowering May–Aug.; flowers yellow, sometimes red at tip of ligules. Chromosomes, $2n = 8$.

Crepis scabra DC., Cat. Monsp. 99. 1813, non Willd.

Borkhausia nicaeënsis Link., ex Spreng., Syst. 3: 653. 1825.

C. adenantha Vis., Flora, 13: 53. 1830.

C. agrestis Fries, ex Bisch., Beit. 269. 1851.

Brachyderea nicaeënsis Sch. Bip., Pollichia, 22–24: 319. 1866.

Berinia nicaeënsis Sch. Bip., loc. cit.

W. Balkan Pen., N. Italy, S.E. France, and S. Pyrenees; montane. Introduced into central and W. Europe and North America (both E. and W.).

The limits of natural distribution are rather indefinite. According to Bischoff (269–271) it is a native of S. France and N. Italy, but in France and S.E. Spain at present it seems to occur only sporadically. Fiori (435) gives the range as France, Dalmatia, Danube reg., Thrace, N. Asia Minor, and Caucasus; whereas Rouy (227) lists Dalmatia, Thrace, Russia, and Caucasus. The inclusion of Asia Minor and the

Caucasus in the range of this species may have been based on Radde's (284) list of xerophytic rock plants from Borshom (west of Tiflis). Except for one cultivated strain, grown from seeds collected in S.E. Bulgaria by Dr. B. Stefanoff, no specimens have been seen by the author from farther east than the W. Balkan reg.,

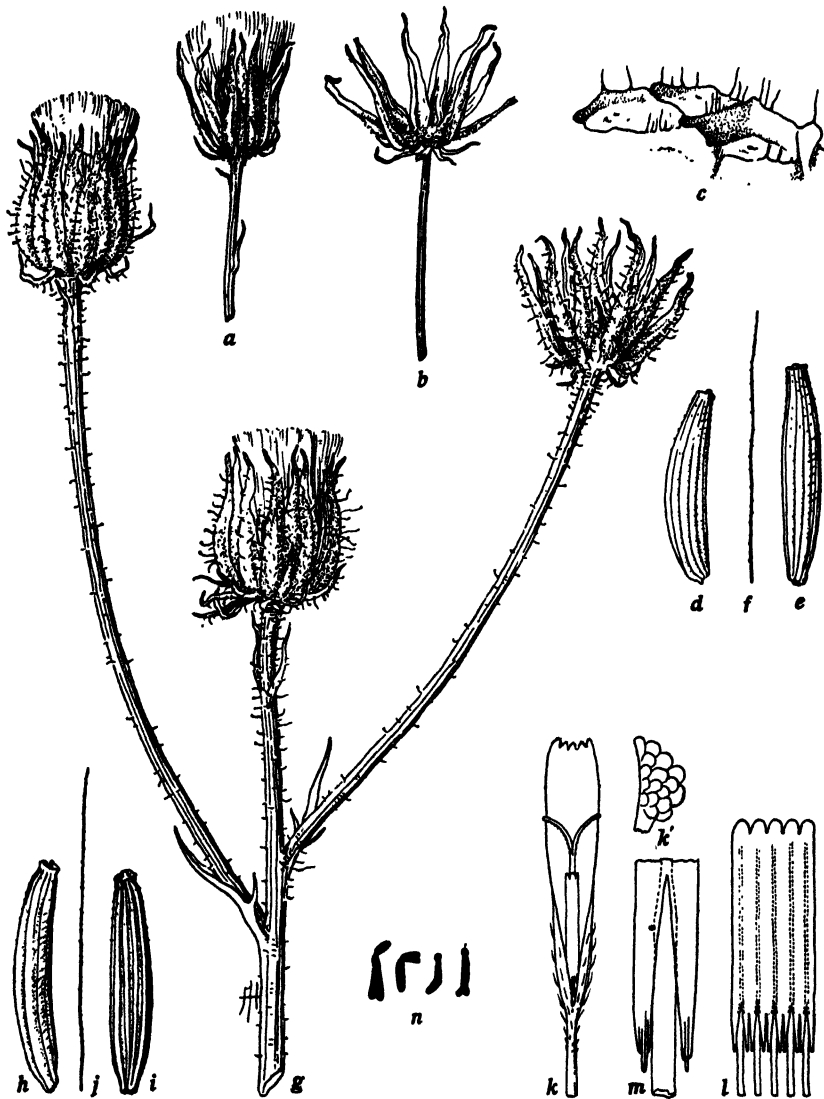


Fig. 251. *Crepis nicaeensis*, a-f, from type (Tor); g-j, from Thellung in 1925 (UC 296062); k-m, from Thellung in 1925 (UC 296063); n, from hort. genet. Calif. 2700 (grown from seeds received from N. Italy through Dr. O. Mattirola): a, head, $\times 2$; b, receptacle and bracts, $\times 2$; c, detail of receptacle, $\times 25$; d-f, 2 achenes and a pappus seta, $\times 8$; g, 3 heads *in situ*, $\times 2$; h-j, 2 achenes and a pappus seta, $\times 8$; k, floret lacking ovary, $\times 4$; k', ligule tooth, lateral view, $\times 32$; l, anther tube, $\times 8$; m, detail of appendages, $\times 32$; n, somatic chromosomes, $n = 4$, $\times 1250$. (See pl. 23.)

where it seems to be of rather general occurrence. Turrill's list of *Crepis* known from the Balkan Pen. reports it from Albania, N. Bulgaria, Serbia, Montenegro, and Dalmatia. With respect to Bulgaria, however, Dr. Stefanoff writes that *C. nicaeensis* is not represented in the Herbarium of the University of Sofia and that

it is very rare and local in that country. Too much should not be inferred from statements made in floras and lists. This plant may easily have been introduced into the Balkan Pen., as into the rest of Europe, with the advent of *Medicago sativa* and other field crops from farther east. But Bischoff states that it is a native of S. France and Piedmont and that it appears to have been introduced into central and W. Europe with foreign grass seed. Visiani (Fl. Dalmatia, 2: 119. 1842-1852 et Suppl. 1: 68. 1871; 2: 55. 1881), however, reports it as indigenous in Dalmatia, and this seems to be corroborated by several collections (cited below) from Albania, Montenegro, and Macedonia. Furthermore, the author has grown at Berkeley typical plants of this species from seed collected, through the kindness of Dr. O. Mattirola of Turin, in the Alps of Bardonecchio, N.W. Italy; and the author has collected it below Sierra del Cadi in the Catalanian Pyrenees at about 1500 m alt., where it was apparently indigenous but rare. Whether it is indigenous in the region between Piedmont and Montenegro and in the Caucasus reg. is very uncertain.

The type is the first specimen cited below under Italy. It appears to have been collected at or near Turin. The type locality as given by Persoon (*loc. cit.*) is around Nice; but Balbis (*loc. cit.*) cites first in *pastures and hills of Tenda*, and, second, *similar places around Nice*.

Balkan Pen.: Macedonia, near Morani, on oak-covered hills below Mt. Ostri, 400-500 m, *Bornmuller 1876* (B); N.E. Serbia, Ceribasa, shrubby hill, in 1884 (Bur); Montenegro, Delaj, Trijepši, Kuči, edge of field, *Baldacci 134* (K, Bur); Dalmatia, Salona, in 1843, ex Prior (K); Albania, Trijepši, subalpine, *Baldacci* in 1902 (B); Albania, in woods, *Baldacci 78* (Bur). **Czechoslovakia:** Vsetin, subspontaneous in sterile field at Lásky, *Bubela* in 1883 (K). **Austria-Hungary:** Mt. Köhegy above Pomáz, among oaks, *Degen* in 1913 (B, Bur); southwest of Wien, near Rodaun, Kaltenleutgeben, in field, *Fleischer* in 1878 (K, Bur); central Hungary, Mt. "Schwabenberg," near Budam, *Borbás* (Bur, Minn); Tirol, Pustaria, near Windisch-Matrei, dry field, 1000 m, *Ausserdorfer* (Bur, Minn). **Germany:** Carlsruhe, wheat fields, rare, *Braun and Doell 2350* (Ms); Palatinate, near Spiram, *Laforet* (Bur); Bavaria, Nürnberg, Grossreuth, wheat field, *Kaulfuss* in 1894 (Po) m.v. 6. **Switzerland:** Nant sur Vevey, *Vetter* in 1876 (Bur); Vaud, Allaman, *Favrat* in 1871 (K); Genève, Fauconnet, ex Munby (K); Grisons, Arosa, *Thellung* in 1925 (UC) m.v. 1; Grisons, Arosa, *Thellung* in 1925 (UC) m.v. 2. **Italy:** Piedmont, Torino, *Balbis* in 1805 (Torino, UC) type; Piedmont, Maritime Alps, Mt. Tenda, *Balbis*, herb. Willd., n. 14734-1 (B); Liguria, Bordighera, Nervia Valley, near Pigna, 300 m, *Bicknell et Pollini* in 1904 (G). **France:** Maritime Alps, Le Bar au Montet, *Pons* in 1889 (K); Haute Loire, between Lempde and Arvant, meadows, 400 m, *Girardet* in 1881 (K); Gers, Masseube, meadows, *Duffort* in 1911 (Bur); Rochefort, meadow, *Crepin* in 1861 (DS); Grenoble, porte du Adieux, *Verlot* in 1870 (Grenoble); Isère, Corence, *Pellat* in 1871 (Grenoble); Hautes Alpes, near Gap, *Pellat* in 1896 (Grenoble); Maine et Loire (Anjou), Chalonnes, in 1818 (K); Var, Draguignan, Pont de Piganières, *Berreymond* (K); Bouches du Rhone, Pic Bretagne, dry meadows, *Roux 2754* (K); Lyon à Montout, *Jordan* in 1840 (Ms); E. Pyrenees, Mt. Villefranche à Belloc, *Sennen* in 1897 (Ms). **Spain:** Catalonia, Na Sra del Mont, *Vayreda* in 1879 (Bur); Catalonia, Baños de S. Vicente dist., above Ansobell village and below Sierra del Cadi, about 1500 m, *Babcock 392* (UC); Catalonia, Pont de Molins, waste land, *Sennen* in 1907 (Bar); Catalonia, Vall de l'Avenco, *Font Quer* in 1920 (Bar). **England:** Yorkshire, Harlow Hill, Harrogate, *Froggett* in 1876 (K); North Yorkshire, Sowerby Fields, meadow, *Froggett* in 1890 (K). **Scandinavia:** Gotland, *Bagenholm* in 1894 (Minn); Holmia, Gronval, *Ahlm* in 1883 (Minn); Denmark, Del, Soudersoen, *Mortensen* in 1870, 1871 (UC). **U. S. A.:** Vermont, Charlotte, *Pringle* in 1875 (G); Massachusetts, Wianno, *Hill* in 1887 (G); Michigan, East Lansing, meadow grown from seed imported from France, *Wheeler* in 1897 (G); Washington, Marysville, fields, *Grant* in 1928 (Wellesley).

Minor Variants of *C. nicaeënsis*

1. (*C. nicaeënsis* var. *laevisquama* Thell., Vierteljahrsschr. Naturf. Ges. Zurich, 55: 286. 1910.) The typical form of the species, at least so far as absence of erect hairs on the involucrel bracts is concerned. The involucre is \pm canescent. Absence of erect hairs from the involucre is doubtless a Mendelian character as contrasted with presence of the same; and probably absence is recessive, since this form, according to Schinz u. Keller (Fl. Schweiz II. Kritische Fl., ed. 3, 361. 1914), is less common than the next. Hairless involucrees were observed among the herbarium specimens

cited above, but no effort was made to assort all the specimens according to these minor superficial characters. *Thellung* in 1925 (UC), Arosa, Grisons, Switzerland.

2. (*C. nicaeënsis* var. *scabriceps* Thell., *loc. cit.*) With unequal yellowish glandular or glandless bristles on peduncle and involucre and \pm canescent involucre, and, according to Schinz u. Keller (*loc. cit.*), the corolla is mostly unicolored and pale yellow. Numerous herbarium specimens have been observed with hairy or finely setose peduncles and involucres, but in the dry state no observations were possible concerning differences in the color of the ligules. This is the most frequent form in Switzerland, according to Schinz u. Keller (*loc. cit.*). *Thellung* in 1925 (UC), Arosa, Grisons, Switzerland.

3. (*C. nicaeënsis* var. *tephrolepis* Thell., *loc. cit.*) Involucre beset with few to many black bristles and densely canescent-pubescent. According to Schinz u. Keller (*loc. cit.*), the corolla is deeper yellow than in m.v. 2 and the ligule teeth are often red. Specimens known to have this particular combination of characters have not been seen by the author.

4. (*C. nicaeënsis* var. *tephrolepis* f. *nigriceps* Thell., ex Schinz u. Keller, *loc. cit.*) Like m.v. 3, except that it lacks the gray pubescence on the involucre and thus reveals the dark green basic color. Specimens have been observed by the author in which the dark green color of the inner involucral bracts is evident, although there is usually more or less gray tomentum.

5. (*C. nicaeënsis* var. *integrifolia* Bisch., *Beit. Fl. Deutsch. u. Schweiz*, 271. 1851.) The lower leaves dentate and the upper subentire. As in many other species, there are varying degrees of dissection of the leaves, from finely denticulate to pinnately parted. If all these variations and combinations of variations were to be recognized by name or number, a needlessly long list of forms would result.

6. The inner involucral bracts sparsely silky-pubescent within. Only one specimen has been observed; but the ventrally glabrous bracts provide such a useful character in distinguishing this species from *C. biennis* that it seems necessary to recognize this form, which may be a hybrid. *Kaulfuss* in 1894 (Po), Germany, Bavaria, Nürnberg, wheat fields near Grossreuth.

Relationship

Whereas *Crepis nicaeënsis* shows considerable resemblance to *C. biennis* of sec. 10 in habit and leaf shape and is, therefore, often confused with that species, yet it actually is closer to *C. capillaris*, especially in the narrow outer involucral bracts and the similarity of the flowers and fruits. This evidence is consistent with the chromosome numbers of the two species. Therefore, *C. nicaeënsis* is placed here as the most primitive species of this section. It must be recognized, however, as a connecting species, since it seems probable that *C. nicaeënsis* was derived from the same ancestral line that produced *C. biennis* (q.v.).

161. *Crepis capillaris* (L.) Wallr.

Linnaea 14: 657. 1840. (Pls. 24, 25, Fig. 252.)

Annual or biennial, 0.2–9 dm high; caudical leaves rosulate, numerous, up to 30 cm long, 4.5 cm wide, lanceolate or oblanceolate, obtuse or acute, mucronate, denticulate, dentate or runcinate-pinnatifid or lyrate-pinnately or bipinnately parted with remote unequal oblanceolate or linear lobes, tapering into a long or short winged petiole with clasping base, glabrous or hispidulous beneath on midrib or \pm hispidulous on both sides with short yellow glandless hairs; lower cauline leaves similar, middle and upper cauline leaves lanceolate, acute, sessile, amplexicaul, acutely auriculate, uppermost linear, bractlike; stem erect, branched above or profusely branched from base upward, or central axis short with numerous semi-erect nearly equal stems, or stems diffuse, semiproscumbent and arcuate, sulcate or striate, \pm hispidulous near base or throughout including peduncles; aggregate inflorescence cymose-corymbiform or paniculate-corymbiform; peduncles 0.5–6.5 cm long, slender or very slender, not much enlarged at base of head, canescent-tomentose like base of involucre or glabrous, sometimes with a few black gland hairs; heads erect, numerous or few in reduced forms, small, 20–60-flowered; involucre cylindric before anthesis, turbinate in fruit, 5–8 mm long, 3–6 mm wide at middle; outer bracts 8, linear, $\frac{1}{3}$ – $\frac{1}{2}$ as long as inner bracts, green or pale and



Fig. 252. *Crepis capillaris*, a-d, from original spec. of *C. polymorpha* var. *stricta* Wallr. (DC); e-l, from original spec. of *C. polymorpha* var. *diffusa* Wallr. (DC); m-t, from Johnston in 1919 (K); u-z, from Daveau in 1883 (Ms); A, from hort. genet. Calif. 899 (grown from seeds collected

scarious, glabrous, tomentose or sparsely gland-hairy, becoming lax; inner bracts 8–16; lanceolate, membranous-margined, canescent-tomentose, often setulose with a double row of short black glandular bristles, becoming dorsally spongy-thickened confluent with the much swollen base of head in fruit, ultimately reflexed, ventrally glabrous; receptacle naked; corolla in marginal corolla 7.5–12 mm long; ligules 1.6–2.5 mm wide, deep yellow, reddish on outer face, pubescent below; teeth 0.2–0.4 mm long; corolla tube 2–3 mm long, pubescent with fine acicular hairs; anther tube yellow, (3) 3.5×1 mm dis.; appendages 0.5–0.6 mm long, lanceolate, acute; filaments 0.6–1 mm longer; style branches 1.15–1.5 mm long, slender, yellow with greenish barbs, sometimes green; achenes brownish-yellow, pale brown or dark brown, 1.5–2.5 mm long, terete or subterete, curved or straight, fusiform or oblong and abruptly narrowed at both ends, with very narrow base and summit and slightly elevated pappus disk, 10-ribbed, ribs narrow, rounded, smooth or finely spiculate near summit, slightly prolonged at base into a small callosity; pappus white, 3–4 mm long, 2-seriate, fine, straight, soft, caducous. Flowering early spring to late autumn under favorable conditions or ephemeral; flowers deep yellow. Chromosomes, $2n = 6$.

Lapsana capillaris L., Sp. Pl., ed. 1, 2: 812. 1753.

Crepis virens L., Sp. Pl., ed. 2, 1: 1134. 1763.

C. tectorum Pollich, Palat. 2: 399. 1777, non L.

C. parviflora Moench, Meth. 535. 1794.

C. neglecta Marsch., Casp. App. 210. 1798, non L.

C. uniflora Thuill., Fl. Paris, ed. 2, vii an. 1799.

C. umbellata Thuill., Fl. Paris 409, *ide* Pers.

C. pinnatifida Willd., Sp. Pl. 3: 1604. 1804, non Fröl., nec Boiss.

C. agrestis Waldst. et Kit., Pl. Rar. Hung. 3: 244. 1812.

C. diffusa DC., Cat. Monsp. 98. 1813.

C. polymorpha Wallr., Sched. Crit. 426. 1822.

C. humilis Gaud., Fl. Helv. 5: 141. 1829.

C. lusitanica Boiss., ex Sch. Bip., in Webb et Berth., Phyt. Canar. 2: 456, 1836–1847.

C. gaditana Boiss., Voy. Bot. Espagne, 743. 1839–1845.

Malacothrix crepidoides A. Gray, ex J. G. Cooper, Pac. R. R. Rept. 12: 53. 1860.

Crepis Cooperi A. Gray, Proc. Am. Acad. 9: 214. 1874.

? *C. Druceana* Murr., ex Druce, Rept. Bot. Soc. Exch. Club Brit. Isles 7: 774. 1926.

S. and middle Europe from Portugal and the British Isles eastward to Lithuania, E. Poland, S.W. Ukraine, Crimea, and the Balkan Pen. Original center of distribution somewhere in central Europe. Frequently adventive along coasts in many parts of the world. Naturalized in W. North America from British Columbia to middle California and eastward into the Cascades and Sierra Nevada in meadows, pastures, and waste places; also along the N. Atlantic coast and St. Lawrence R.; often reported as a serious lawn pest. Adventive and possibly naturalized on the W. coast of South America and in Australia.

Critical Specimens

In the Linnaean herbarium no specimen of *Lapsana capillaris* was found, nor was an authentic specimen of *C. virens* found, but *Crepis* folio no. 19 was determined as *C. virens* by Schultz Bipontinus. From Linnaeus' description, however, it appears

near Eureka, Calif., by Dr. J. P. Tracy): *a*, branchlet with 2 heads, $\times 2$; *b*, an old head, $\times 2$; *c*, *d*, achene and pappus seta, $\times 8$; *e*, flowering head, $\times 2$; *f*, fruiting head, $\times 2$; *g*, old head, $\times 2$; *h*, floret lacking ovary, $\times 4$; *h'*, detail of ligule tooth, $\times 50$; *i*, anther tube, $\times 8$; *j*, detail of appendages, $\times 32$; *k*, *l*, achene and pappus seta, $\times 8$; *m*, flowering head, $\times 2$; *n*, fruiting head, $\times 2$; *o*, floret lacking ovary, $\times 4$; *o'*, detail of ligule tooth, $\times 50$; *p*, anther tube, $\times 8$; *q*, detail of appendages, $\times 32$; *r-t*, 2 achenes and a pappus seta, $\times 8$; *u*, part of aggregate inflorescence, $\times 1$; *v*, floret lacking ovary, $\times 4$; *v'*, detail of ligule tooth, $\times 50$; *w*, anther tube, $\times 8$; *x*, detail of appendages, $\times 32$; *y*, *z*, achene and pappus seta, $\times 8$; *A*, somatic chromosomes, $n = 3$, $\times 1250$.

that he had a many-stemmed form similar to that described by Wallroth as *C. capillaris*, although apparently the latter did not know of Linnaeus' earlier publication of the name. In the Willdenow herbarium no specimen of *C. pinnatifida* was found; Willd. no. 14751 is an authentic specimen of *C. agrestis* W. et K. (see m.v. 6). In the de Candolle herbarium is an authentic specimen of *C. polymorpha* var. *stricta* Wallr. (see m.v. 7) and one of *C. polymorpha* var. *diffusa* Wallr., which is also labeled *C. diffusa* DC. This is closely similar to the type of *C. capillaris* Wallr. in the herbarium of the National Museum in Prag. Since it agrees with Linnaeus' description and since Linnaeus himself later referred *Lapsana capillaris* to *C. virens*, this low, diffuse, small-headed form must be considered as typical of the species (see m.v. 1).

Variability

Polymorphic and rich in ecads and genetic forms, this remarkable species, with the smallest chromosome number yet reported in the Angiosperms, has been able to adapt itself to conditions ranging from those in semiarid S. Spain to highly humid Great Britain and to similar conditions on the Pacific Coast of North America. It sustains itself at sea level and at altitudes of 1200 m or more; in moist, rich, and in dry, sterile soils; in shade or full sun; and when undisturbed or when subjected to frequent cutting in lawns. The chief limiting factors, apparently, are available soil moisture and degree of winter cold, as it flourishes best in climates having only moderately cool winters and abundant rainfall. Despite the high variability of this species and the large number of types, which have been named in all categories from forma to species, there appear to be no natural groups within the inclusive species which are distinguishable by a sufficient number of constant differences to warrant their recognition as subspecies. So numerous, indeed, are the names of varieties and forms based on such minor variations as degree of dissection of the leaves that no attempt has been made to list all of them. Only the more important named variants are listed below by number together with certain other outstanding variants noted by the present writer.

It should be remembered that these apparently distinct forms are all connected by intergrading variants representing either different genetic combinations or ecological modifications. Statistical study supports this view. For example, the length of involucre and width of involucre at the receptacle in specimens on 66 sheets of *C. capillaris* collected in Europe (in Herb. Kew) were measured and tabulated according to habit of plant and geographical regions. The results of this study may be summarized as follows: in 16 specimens of m.v. 1 the involucre averaged 4.9 mm long \times 2.4 mm wide; these were distributed nearly throughout the range of the species, i.e., from Portugal to Bohemia. There were 14 specimens, not m.v. 1, all from southern points in the range of the species which averaged 5.2×2.6 mm. The remaining 36 specimens were distributed from central France through N. Italy and Switzerland to Tirol, Austria, Germany, Scandinavia, and British Isles; they averaged 6.3×3.9 mm. Thus, in this particular lot of plants there appears to be a definite tendency toward larger size in the northern part of the range. But this is easily accounted for on the basis of such ecologic factors as available moisture and character of soil, especially the former. Moreover, occasional specimens of the larger forms occur from the southern part of the range. Hence, there seems to be no satisfactory basis in comparative morphology and natural distribution for the recognition of subspecies.

At the same time, it must be noted that there is experimental evidence that genetic differentiation is taking place in this species. A cross between a low diffuse form

(hort. genet. Calif. 1816) from the Pyrenees and a robust form (hort. genet. Calif. 793) from the Copenhagen Botanic Garden produced hybrids intermediate in size, characters, and habit, and not over 50 per cent fertile. This indicates genetic diversity between the parent forms affecting both morphological characters and physiological qualities. But it is possible that equal genetic diversity exists between forms occurring at different localities in either the southern or northern parts of the species' range. For the present it is sufficient to recognize this tendency toward differentiation and segregation of distinct groups in different regions. It is not improbable, however, that future investigations will prove the existence of geographically separated groups possessing sufficient constant genetic differences to warrant their recognition as subspecies.

Portugal: Ericeira, sandy beach, Welwitsch (K) m.v. 1; Alfeite, sandy field, *Daveau* in 1879 (G) m.v. 5; Berlenga Is., *Daveau* 1380, 1089 (Mo) variants; Azores, Fayal, *Brown* 162 (G) m.v. 3. **Spain:** Gibraltar, Palmones Pinar, *Wolley-Dodd* 1930 (K) m.v. 6; Cadiz, *Boissier* (K) m.v. 5; Gerona, Vidreras, *Giberta* in 1909 (Bar) m.v. 8; Puerto Santa Maria, sandy beach, *Bourgeau* 309, 310 (K) m.v. 1, 5; Algeciras, between Castellar de la Frontera and Almoraima, sandy clearings in corkwoods, *Hubbard* 699, 712 (K) m.v. 5, 8; Granada, Jajo de Alhama, *Porta et Rigo* 501 (K) m.v. 1; Catalonia, Montagut, Aug., 1872 (Bar, UC) m.v. 1; Catalonia, near Vic, *Masferrer* in 1870 (Bar) m.v. 5; Leon, near Riaño, meadow, *Lacaita* 526 (UC) m.v. 7; Leon, Mansilla, sterile soil, *Lacaita* 498 (BML) m.v. 1. **France:** Basse-Pyrenees, Eaux-Chaudes, route de Gabas, *Pellat* in 1899 (Grenoble); Lot-et-Garonne, Agen, *Gandoger* in 1910 (K) m.v. 2; Haute-Saône, La Neuville, *Bertrand* in 1844 (Grenoble) m.v. 1; Aude, Carcassone, *Pellat* in 1866 (Grenoble); Montpellier, Lauret, *Martins* in 1860 (K) m.v. 7; Gironde, Pessac, in 1814 (DS) m.v. 2; Gard, St. Paule-Coste, *Jordan* in 1869 (Bur) m.v. 7; Aude, Bages, *Pau* in 1912 (Bar) m.v. 8; Oise, Fleurines, July, 1824 (DS) m.v. 7; Moselle, Nancy, *Lussenue* in 1829 (DS) m.v. 7; Savoy, Albens, Mt. Merderie, in 1890 (K) m.v. 7; Bauvais, near Bellovaco, dry sand, July, 1817 (DS) m.v. 3, 7. **Italy:** Rome, Gradoli, in 1897 (Rome) m.v. 8; Florence, alla Concezione, *J. Ball* in 1848 (G) m.v. 2, 8; Piedmont, Val di Pesio, dry banks below Certosa, *Lacaita* in 1882 (BML) m.v. 5; Longobardia, Sondrio, fields and waysides, *Fiori et Béguinot* 1180 (G) m.v. 7. **Greece:** Laconia, littoral reg. of Mt. Selitza near Kalamata, *Zahn* in 1896 (Bur) m.v. 1. **Hungary:** without locality, *Willdenow* 14751 (BW) m.v. 6. **Czechoslovakia:** near Prag, *Tausch* 920 (PM) m.v. 6. **Austria:** Schwertberg, *Keck* (UC) m.v. 1, 2; Schwertberg, *Keck* in 1872 (UC) m.v. 5; Stiria, near Sau- retsch, *Derder* in 1870 (K) m.v. 2; Tirol, Lienz, *Gander* in 1870 (K) m.v. 2. **Germany:** Thuringia, between Naumburg and Helbra, *Wallroth* (PM) m.v. 1; Thuringia, *Wallroth* in 1822 and 1828 (DC, Ucf, K) m.v. 1; Thuringia, *Wallroth* in 1822 (DC, Ucf type of *C. polymorpha* var. *stricta*) m.v. 7; Munich, *Schultz* in 1837 (K) m.v. 6; Palatinate, near Deidesheim, *F. W.* 32 (K) m.v. 3; Berlin, Tegel, *Woller* in 1900 (Minn) m.v. 7. **Switzerland:** Vaud, near Vevrey, *Blanchet* in 1864 (K) m.v. 1; Baden, Lörrach, Bogenhard in 1850 (Minn) m.v. 6. **Sweden:** Gotl. I., Vithy, *Möler* (Bur); Oeland I., in Farjestaden, *Engstrom* in 1869 (K) m.v. 5; Oeland I., *Ekstrand* in 1875 (Minn) m.v. 7; Besten, Springstr., *Luhr* in 1866 (Minn) m.v. 6. **Netherlands:** Seelandia (G) m.v. 1; near Kampen (G) m.v. 7. **British Isles:** England, Derwen, Corwen, *Harnaman* 1497 (Oxford-Druce) m.v. 9; England †, between Cavisbrooke and Swainston, *Bromfield* (K) m.v. 4; England, Kew green, *Hughes* in 1922 (K) m.v. 1; England, Cheshire, near Oxtan, *Lomax* in 1891 (DS) m.v. 6; Scotland, Garson, Stromnes, Mainland, Orkney, *Johnston* in 1919 (K) m.v. 3. **Canada:** Ontario, Wingham, *Morton* in 1895 (Po, RM, DS) m.v. 8. **Maine:** Orono, *Fernald and Long* (G) m.v. 4. **Massachusetts:** Barnstable Co., Harwich, *Fernald and Long* 17648 (FM); Harwich, *Fernald* 17647 (G) m.v. 6. **New York:** Tompkins Co., Ithaca, Cayuga Heights, *Eames and MacDaniels* 5340 (G) m.v. 6; Hunter's Point, *Brown* in 1879 (G) m.v. 3. **New Jersey:** Oceanic, *Knipe* in 1892 (G). **British Columbia:** Vancouver I., Alberni Valley, *Kellogg* in 1910 (UC) m.v. 6; Chemaines, *Pineo* in 1900 (UC) m.v. 6, 7; Glacier, *Dudley* in 1896 (DS) m.v. 7. **Washington:** San Juan Is., Friday Harbor, *Zeller* 959 (DS) m.v. 7; Pacific Co., Long Beach, *McGregor* in 1907 (DS) m.v. 11; Clark Co., *Suksdorf* 29 (G) m.v. 3; Klickitat Co., Bingen, *Suksdorf* 5171 (FM, DS) m.v. 7. **Oregon:** Cooper in 1853 (G, type material of *Malacothrix crepoides*) variants; Marion Co., Salem, *Hall* 327 (K, G, FM); Portland, Willamette Heights, *Sheldon* 11173 (DS) m.v. 8; Clackamas Co., Oswego, *Nelson* 1246 (G) m.v. 10; Douglas Co., Calapooya Valley, *Barber* 92 (G) m.v. 3; Columbia Co., Beaver Creek Falls, *Abrams* 8836 (DS) m.v. 6; Deschutes Co., Redmond, field near aqueduct, *Whited* 249 (DS) m.v. 6. **California:** Del Norte Co., Lake Earl, *Parks* in 1925 (UC) m.v. 6; Humboldt Co., near Fortuna, fields, *Abrams* 8234 (DS) m.v. 6; Mendocino Co., near Mendocino, *Davy* 6099 (UC) m.v. 6; Alameda Co., Berkeley, *Lawson* in 1897 (DS) m.v. 6; Los Angeles Co., Rock Creek, *Davidson* in 1893 (DS) m.v. 7;

Siskiyou Co., Sisson, *Eastwood* 1176 (G) m.v. 7; Shasta Co., Goose Valley, *Eastwood* 923 (G) m.v. 7; Plumas Co., Meadow Valley, *Babcock and Navashin* 138 (UC) m.v. 3, 7; Tuolumne Co., Hetch Hetchy Valley, *Jones* 610 (UC) m.v. 7. Nevada: Reno, *Hillman* (Po).

Minor Variants of C. capillaris

1. (*Lapsana capillaris* L., *loc. cit.*; *Crepis uniflora* Thuill., *loc. cit.*; *C. polymorpha* var. *diffusa* Wallr., *loc. cit.*, *C. capillaris* Wallr., *loc. cit.*) Low diffuse plants with numerous slender semi-procumbent stems, filiform peduncles, and very small heads (about 20-flowered); involucre 4.5–5 mm long, 1.5–2.5 mm wide at receptacle. Considered, no doubt rightfully, by Bischoff (278) and other critical workers as merely ecologic forms resulting from mutilation. In fact, the types of *C. capillaris* Wallr. (PM) and *C. polymorpha* var. *diffusa* Wallr. (DC, K) both have the appearance of being such a variant (pl. 24, a). Similar ecads are believed to result from other conditions, such as drouth and sterile soil, but the genetic nature of these plants is unknown; examples come from Portugal, hills near Puerto Santa Maria, *Bourgeau* 309 (K; pl. 24, c), and from Spain, Mansilla, *Lacaita* 498 (BML; pl. 24, d). Similar forms known to be hereditary and to result from a single gene mutation have also come to light in the course of genetic investigations on this species. This makes it very probable that such an apparently normal plant as *Blanchet* in 1864 (K) from Vervay, Switzerland (pl. 24, b), is also genetically different from single-stemmed forms. Other specimens of this variant are: *Welwitsch* (K), sandy beach, Ericeira, Portugal; *Lacaita* 498 (BML), sterile soil in sandy pasture, Leon, Mansilla, Spain; *Bertrand* in 1844 (Grenoble), La Neuville, Haute-Saône, France; *Zahn* in 1896 (Bur), littoral reg. of Mt. Selitza, near Kalamata, N.W. Laconia, Greece; *Wallroth* (PM), between Naumburg and Helbra, Thuringia, Germany; *Wallroth* in 1822 and 1828 (DC, K), Thuringia, Germany; *Hughes* in 1922 (K), Kew green, England.

2. Intermediate to the single-stemmed forms; up to 3 dm high, very slender, cauline leaves small, heads like those in m.v. 1. The habit is semidiffuse, i.e., it has 2 or more rather weak stems, slender paniculate branches, and filiform peduncles. *J. Ball* in 1848 (G; pl. 24, e), near Florence, Italy; *Gandoger* in 1910 (K), Agen, France; *Brandegee* (DS), Berkeley, California.

3. (*C. cooperi* A. Gray, *loc. cit.*) Resembles m.v. 1 in habit, but more robust throughout and hence intermediate to the largest diffuse and single-stemmed forms. Probably an ecad, resulting from mutilation at an early stage. *Babcock and Navashin* 138B (UC; pl. 25, a) border of meadow, Meadow Valley, Plumas Co., California; *Johnston* in 1919 (K), artificial meadow, Orkney, Mainland, Scotland; *Suksdorf* in 1882 (G, type of *C. Cooperi* Gray), Fisher's Landing, Clark Co., Washington.

4. Resembles m.v. 3, but still more robust, 3.5–4.5 dm high; with many robust stems, the central one a little stouter; leaves up to 6 cm wide, bipinnate; heads large, many-flowered; involucre 7–8 mm long; achenes 2.5 mm long, rather strongly ribbed, ribs simulating those of *C. nicæensis* but only half as wide. Probably an ecad, resulting from highly favorable growth conditions; possibly a polyploid form. Ex herb. *Bromfield* (K; pl. 25, b), roadside between Cavisbrooke and Swainston, England (†); *Fernald and Long* 14892 (G), Orono, Maine.

5. Plant with strong central axis and numerous long branches from base or near base, 2.5–5.5 dm high; heads medium; involucre 4.5–6.5 mm long. *Bourgeau* 310 (K; pl. 24, g), sandy beach, Puerto Santa Maria, Spain; *Font Quer* in 1925 (UC), near Cadiz, Spain; *Lacaita* in 1882 (BML), below Certosa, Piedmont, Italy; *Daveau* in 1879 (G), sandy fields, Alfeite, Portugal; *Duncan* 317 (DS), fields near Requa, Del Norte Co., California.

6. (*C. agrestis* W. et K., *loc. cit.*; *C. virens* L. var. *agrestis* Bisch., *Beit. Fl. Deutsch. Schweiz*, 277. 1851; *C. virens* L. var. *elatior* Car. et St. Lag., *Fl. Moyen, Rhone et Loire*, 501. 1889, incl. syn.) Plants robust, 3–9 dm high, with erect leafy stem, oblanceolate or lanceolate leaves and subcorymbose aggregate inflorescence; heads numerous, large, as in m.v. 4. *Schultz* in 1837 (K; pl. 25, c), Munich, Germany; *Wolley-Dodd* 1930 (K), Palmones Pinar, Gibraltar; *Davy and Blasdale* 5537B (UC), near Scotia, Humboldt Co., California; *Fernald* 17647 (G), Harwich, Barnstable Co., Mass.; *McGregor* in 1924 (DS), near Requa, Del Norte Co., California.

7. (*C. polymorpha* var. *stricta* Wallr., *Sched. Crit.* 426. 1822; DC., *Prod.* 7: 162. 1838, incl. syn. †) Stem erect, 4 dm high, less robust than the preceding, like peduncles glabrous or nearly so; involucre 6–8 mm long. *Wallroth* in 1822 (DC, type of *C. polymorpha* var. *stricta*; pl. 24, f), Thuringia, Germany; *Schultz Bip.* 122 (K), Deidesheim, Germany; *Tracy* 4961 (UC), Holmes Flat, Humboldt Co., Calif.; *Eastwood* 923 (G), Goose Valley, Shasta Co., Calif.; *Suksdorf* 5171 (DS), near Bingen, Washington.

8. (*C. humilis* Gaud., *loc. cit.*; *C. polymorpha* var. *humilis* DC., *Prod.* 7: 162. 1838, incl. syn. †) Stem erect, subcorymbosely branched above, like the leaves ± hispidulous or glabrous; lower leaves lanceolate or oblanceolate, runcinate, dentate or denticulate; heads rather small. Among the 14 specimens filed under this name in Herb. DC. are several forms with other names; none is

acceptable as the type. De Candolle, however, indicates that it varies into a 1-headed form with linear leaves, and this, like the name, implies a reduced form with single erect stem. *Hubbard 712* (K; pl. 25, d), sandy clearings near Algeciras, Spain; *Ciberta* in 1909 (Bar), Videras, Gerona, Spain; *Morton* in 1895 (Po, RM, DS), Wingham, Ontario, Canada.

9. (*C. capillaris* var. *anglica* Druce et Thell., Rept. Bot. Exch. Club, 7: 42. 1924.) Plant very robust, upper cauline leaves 17–27 cm long; heads large; involucre 1 cm broad in pressed condition; achenes large. Possibly a polyploid form. According to the authors, this variant is widely distributed in Britain southward from Orkney, and it has been mistaken for *C. nicaeensis* Balb. (cf. m.v. 12). *Harnaman 1497* (Oxford-Druce), Corwen, Derwen, England.

10. Near m.v. 3, but greatly modified by ecologic conditions. Leaves mostly caudical, semi-erect, up to 10 cm long, 1 cm wide, oblanceolate, obtuse, runcinate-pinnatifid, petiolate; stems 2–5, scapelike, 1-headed or with a few abortive heads lower down; flowering heads large, many-flowered; involucre 8 mm long, 5 mm wide at base; florets 9–10 mm long; anther tube 3.5 mm long; style branches 1.5 mm long, greenish; (achenes lacking); pappus 3–4 mm long, fine, white. *Nelson 1246* (G), railroad track, Oswego, Clackamas Co., Oregon.

11. Simulates m.v. 1, but with rather stiff arcuate stems and peduncles; heads medium to large, many-flowered; involucre 6–7 mm long, 4 mm wide at receptacle; corolla 9 mm long; anther tube 3 mm long; style branches 1.5 mm long, greenish; achenes 1.75–2.25 mm long. Probably a reduced state of m.v. 5, 6, or 7. *McGregor* in 1907 (DS), Long Beach, Pacific Co., Washington.

12. (*C. Druceana* Murr., loc. cit.) Although a specimen has not been seen, and although it is suggested by the author that it may be a hybrid between *C. capillaris* and *C. biennis*, yet it seems more probable that it is merely another giant form of *C. capillaris*, probably polyploid, like m.v. 9. The original description reads: "Verisimiliter *C. biennis* × *C. capillaris*. Ramificatis et folia ut in *C. capillaris*; squamae obscurae subglabrae basim versus perciassime floccosae; capitula tripla, majora; ligulae apice rubristriatae." Collected at Frilford, Berkshire, England.

Relationship

Considered morphologically, *Crepis capillaris* finds its closest relatives in *C. parviflora* and *C. neglecta*, on the one hand, and *C. nicaeensis*, on the other. Genetic forms of *C. capillaris* are known which have achenes quite as small as those of *C. parviflora*, whereas the largest known achenes of *C. capillaris* (see m.v. 4) resemble those of *C. nicaeensis* somewhat, although they are definitely smaller. From these species it is sharply set off, however, by numerous characters and by having 3 instead of 4 haploid chromosomes. The chromosomes of *C. capillaris* and *C. parviflora* are generally similar, but the chromosomes of *C. neglecta* are evidently narrower than those of either *C. parviflora* or *C. capillaris*, and on morphological grounds *C. neglecta* is less close to *C. capillaris* than to *C. parviflora*. But the chromosomes of *C. nicaeensis* are very similar to those of *C. capillaris*, except for the extra pair which are different from any of the 3 pairs of *C. capillaris*. Another species having 3 pairs of chromosomes is *C. Zacantha*; and, except for the very large satellites, its chromosomes are rather similar to those of *C. capillaris*. But *C. Zacantha* is a very different species, being more closely allied to *C. Dioscoridis*.

162. *Crepis parviflora* Desf.

Ex Pers., Encheir., 2: 376. 1807. (Fig. 253.)

Annual, a few centimeters to 1 m high; root vertical, tapering; caudex simple, leafy; caudical leaves oblanceolate, acute, coarsely runcinate with few broad triangular acute lateral lobes, attenuate into a narrowly winged petiole, densely pubescent with pale setiform glandless hairs; cauline leaves numerous, lanceolate, acute or acuminate, dentate to entire, sessile, mostly sagittate-amplexicaul, auricles acute or acuminate, uppermost bractlike, pubescent; stem erect, terete, striate or sulcate, hispidulous or pubescent below, glabrescent above, paniculately branched from base upward or only above or many-branched from base, thus forming an erect densely bushy plant, branches cymose-corymbiform, many-headed; peduncles short, very slender, glabrous or tomentulose; heads erect, very small, 20–30-flowered; involucre cylindric-campanulate in anthesis, conical or reflexed at maturity,

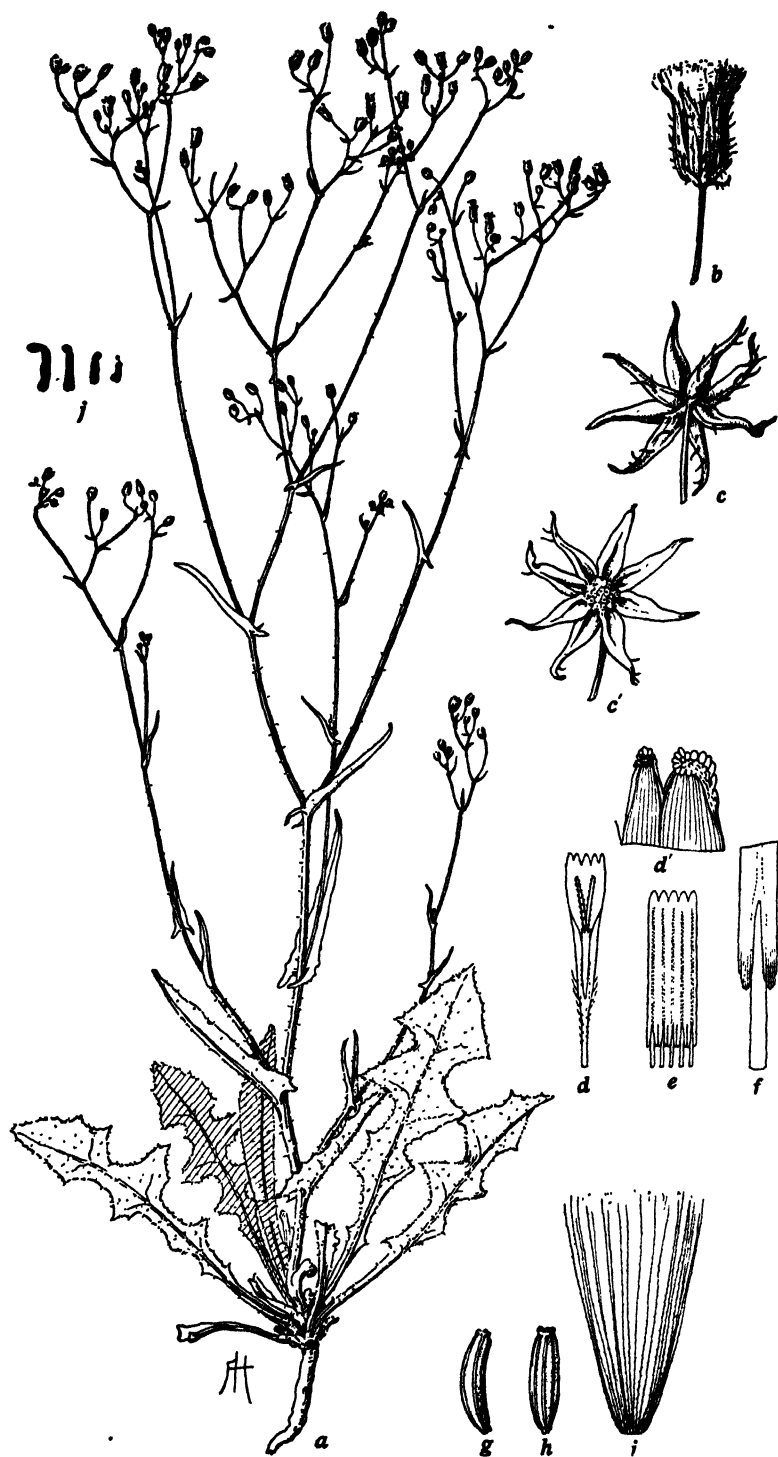


Fig. 253. *Crepis parviflora*, a, from Hall 12522 (UC 346481); b-i, from Krause 3362 (UC 463861); j, from hort. genet. Calif. 1630 (grown from seeds received from Tiflis, Georgia, through Dr. M. Navashin): a, plant, $\times \frac{1}{2}$; b, fruiting head, $\times 2$; c, c', old head with bracts spread open, outer and inner faces, $\times 2$; d, floret lacking ovary, $\times 4$; d', detail of ligule teeth, $\times 50$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g-i, 2 achenes and pappus, $\times 8$; j, somatic chromosomes, $n = 4$, $\times 1250$.

4–6 mm long, 2–4 mm wide; outer bracts 5, nearly equal, $\frac{1}{3}$ as long as inner bracts, linear, acute, somewhat carinate, glabrous, tomentulose or setulose; inner bracts 8–10, in 2 series, alternately wider and narrower, lanceolate, acute, glabrous on inner face, with a median dorsal row of pale glandless setules and/or canescent-tomentulose; receptacle areolate-fimbriate, fimbriae low, thin; corolla 6–10 mm long; ligule 1.3–2.25 mm wide; teeth 0.1–0.4 mm long, the tips green or red; corolla tube 2–2.25 mm long, pubescent like base of ligule, with fine acicular hairs 0.02–0.5 mm long; anther tube (2) 2.25 \times 0.8 mm dis., yellow; appendages 0.35 mm long, oblong, acute; filaments 0.3–0.4 mm longer; style branches 1.5 mm long, 0.1 mm wide, green; achenes stramineous or tawny, 1.4–2 mm long, 0.4–0.5 mm wide, subterete, columnar, slightly attenuate to the narrow pappus disk, strongly constricted at the very narrow base, 10-ribbed, ribs equal, narrow, rounded, smooth; pappus white, 2.5–4 mm long, 1-seriate, very fine, soft, deciduous, coming away in a ring or in sections. Flowers yellow, with or without red on outer face of ligules; style branches green. Chromosomes, $2n = 8$.

Non *Crepis parviflora* Moench, Meth. 535. 1794 = *C. capillaris*.

Crepis muricata Sibth. et Sm., Prod. 2: 138. 1813.

C. parviflora Jacq., ex Spreng., Syst., ed. 16, 3: 634. 1826.

Geracium parviflorum Rehb., ex Moessl., Handb., ed. 2, 2: 1368. 1829.

C. breviflora Del., ex Steud., Nom., ed. 2, 1: 436. 1840.

C. fuliginosa Fleischer, ex Sch. Bip., in Webb et Berth., Phytog. Canar. 2: 455. 1836–1850 in syn., non Sibth. et Sm.

E. Mediterranean reg. from Egypt northward through Palestine, Cyprus, Rhodes, Syria, Turkey, Aegean Archipelago, E. Greece, and eastward to the Caucasus and N. Persia. Introduced in S. France and the Canary Is. Lowlands.

This species is highly variable in size and habit of the plant, as well as in size of heads and florets and degree of hispidity of leaves, stem, and involucre. Associated with larger size of the plant is a tendency to develop a single strong axis which is branched above or from base to summit. Strongly contrasted with plants of this habit are plants of lower stature which are many-branched from the base, thus forming low densely bushy plants which usually have smaller heads and florets. From the evidence available it has been impossible to determine that either of these habit forms is a distinct geographical race. Numerous collections have been seen which consist exclusively of either one form or the other or of much reduced plants which cannot be assigned to either form. But there are two collections, one from Fedmin, Egypt (Schweinfurth no. 133), the other from Bijokarpaso, Cyprus (Haradjian no. 234), which contain plants of both habit forms. These collections show that the two forms occur together at two widely separated localities, from which we may infer that these habitual differences, although striking, have a rather simple genetic basis. Plants of both forms have been cultivated but no genetic experiments have been attempted. It has been observed, however, that cultivated plants of the tall form are highly self-sterile, whereas plants of the low form are self-fertile. From the preponderance of collections consisting only of the tall form, it would appear that this is the normal, widely distributed type of the species. From Desfontaines' description it is clear that this is the type on which his description was based. Moreover, the 5 sheets of specimens in herb. DC. Prod. iii: 162, no. 11, are all this form. Therefore, the low bushy small-flowered type may be considered as a mutant form which appears spontaneously in nature. It has evidently been introduced into S. France, and it has appeared in botanical garden collections. It will be referred to below as m.v. 1; but in the citation of specimens the omission of this designation does not necessarily imply that the plant in question is typical,

because fragmentary and much reduced specimens cannot be determined with certainty. Specimens which are clearly typical are so designated.

Egypt: *Delile* (Ms, UCf) as *C. breviflora*; Fajum, Fedmin, *Schweinfurth 133* (K) typical and m.v. 1; Nile Valley, *Schweinfurth* in 1887 (Genoa) typical; Tantau, *Muschler* in 1906 (K). **Palestine:** Dead Sea, Ghor-es-Safiyeh, *Meyers and Dinsmore 5845* (K). **Cyprus:** Bijokarpaso, *Haradjian 234* (DL) typical and m.v. 1; near St. Hilarion, *Sintenis and Rigo 283* (K) m.v. 1; Agricultural Experiment Station, *Waitsinger* in 1933 (UC) typical. **Turkey:** Cilicia, Anamour, *Cosson 59* (K) typical; Lydia, Smyrna, *Fleischer* in 1827 (K) typical; *ibid.*, Göstepe, *Bornmüller 9731* (K); Dumbrek Valley, Renkvei (†), *Sintenis 197* (K); Pontus, W. Samsun, *Krause 3921* (UC) typical; Pontus, near Çukurbük, south of Samsun, *Krause 3862, 3882* (UC) typical; Pontus, near Tutsal, *Krause 3790* (UC) typical. **Aegean Archipelago:** Scarpanto (= Karpathos), Olympus, *Forsyth Major 30* (Bo) typical; Scarpanto, Athos, *Pichler 420* (Bo) typical; Astypalaea, *d'Urville* in 1820 (DC) typical. **Greece:** *Haller 32* (Oxford-Druce) as *C. muricata*; Argolis, Kassos, near Argos, *Forsyth Major 322* (Bo); Thessaly, *Adamovic* in 1906 (K) typical; Dalmatia, Meleda I., Addolorata Cemetery, *Penza* in 1925 (Wellesley). **Iraq:** Bagubeh, Testing Station, *Graham* in 1920 (K) typical. **Caucasus:** *Radde 346* (K) typical, except for the nonsetose involucre. **Transcaucasia:** Azerbaijan Prov., Geortschai dist., Koromaijan, near the village Aral-Vechtiber, *Karjaze* in 1929 (G) involucre glabrous. **France:** Montpellier (†) port (Juvenal †), *G* (= *Godron* †) *208* (Ms) m.v. 1 (†); Var, Cap Brun, near Toulon, *Hall 21522* (UC) typical.

Relationship

Crepis parviflora is closest to *C. capillaris* but is usually distinguished from that species by the entire or denticulate cauline leaves and their acuminate sagittate auricles, and by the strongly setulose leaves, stems, and involucre. In size of heads, florets, achenes, and pappus the two species overlap, and in reduced forms the cauline leaves may not be characteristically developed. In such forms, if the characteristic pubescence is lacking, the color of the style branches will generally suffice. In *C. capillaris* these are usually yellow (though in a few forms they are greenish or green), whereas in *C. parviflora* they are green. The two species occupy different, though adjacent, geographic areas; and the chromosome numbers differ (*C. parviflora*, $n = 4$; *C. capillaris*, $n = 3$).

It has been suggested (Babcock and Navashin, *Bibliog. Genetica*, 6: 28. 1930) that *C. parviflora* may have originated from *C. capillaris* by fragmentation of one of the three *C. capillaris* chromosomes. But there are several objections to this hypothesis. An important one is the fact that recent cytogenetic research has practically proved that the 3-paired *Crepis* species have been derived from 4-paired ancestors. The two species are sufficiently alike genetically so that they can be crossed artificially, producing sterile hybrids. But the results of crossing both species to a third species (Babcock and Navashin, *op. cit.*, 61) indicate that they differ in certain genetic factors. It is more plausible to assume that the two species were derived from a common ancestor with 4 pairs of chromosomes.

163. *Crepis insignis* sp. nov.

(Plate 26. Fig. 254.)

Herba annua, caulibus numerosis circa 0.5 dm altis, rosella circa 1.8 dm lata; folia caudicalia numerosa, ad 9 cm longam 2 cm latam, oblanceolata acuminata pinnatifida vel bipinnatifida tomentulosa et puberula, rachi tenui, segmentis tenuis acuminatis lateralibus ad petiolum alatum irregulariter parvioribus, segmentis et dentibus corneo-mucronatis; folia caulina similia vel sessilia ad basim laciniatis vel linearia integris; caules numerosi tenues scapiformes vel 1-3-furcati, ramis pedunculatis interdum bicepitibus; capitula erecta parva circa 40-flora; involucre campanulatum in anthesim circa 6 mm altum 4 mm latum, squamis exterioribus 5 circa $\frac{1}{2}$ interiorum aequantibus ovatis acutis glabris scariosis, squamis interioribus

8–9, ovato-lanceolatis acutis, apice albo-ciliatis, medio-dorso valde setulosis, setis bicoloribus, ventre glabris; corolla 7–8 mm longa, ligula 1 mm lata, dentibus 0.2–0.4 mm longis, tubo 2.5 mm longo glabro; antherae flavae circa 2.7 mm longae appendicibus 0.5 mm longibus lanceolatis acutibus, filamentis 0.3 mm longioribus; rami styli 1.5 mm longi 0.1 mm lati flavi; achaenia valde immatura 1.5 mm longa 0.4 mm lata fusiformia, sub discum pappiferum expansum valde constricta, 10-striata minutissime spiculata; pappus albus 2.5 mm longus 1–2-seriatus tenuissimus mollis deciduus.

Annual, with numerous stems about 0.5 dm high and a dense rosette about 1.8 dm wide; caudical leaves numerous, up to 9 cm long, 2 cm wide, oblanceolate, acuminate, pinnately or bipinnately parted with narrow rachis and remote narrow acuminate

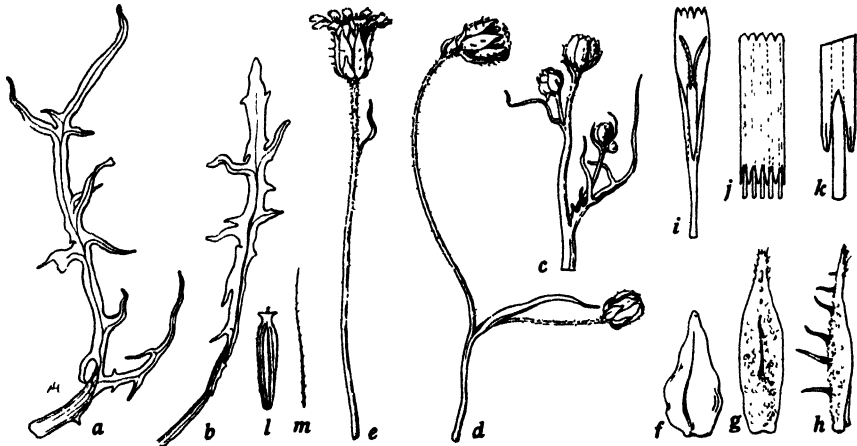


Fig. 254. *Crepis insignis*, from type (DL): *a*, *b*, rosette leaves, $\times 1$; *c*, *d*, details of inflorescence, $\times 1$; *f*, outer involucre bract, outer face, $\times 4$; *g*, *h*, inner involucre bracts, outer face showing bicolored setae, $\times 4$; *i*, floret lacking ovary, $\times 4$; *j*, anther tube, $\times 8$; *k*, detail of appendages, $\times 32$; *l*, *m*, immature achene and pappus seta, $\times 8$. Cf. pl. 26.

segments, lateral segments irregularly reduced toward the broadly winged 3–5-veined petiole, sparsely tomentulose and puberulent, lobes and teeth corneous-mucronate; cauline leaves similar or sessile and laciniately lobed near base or linear, entire and bractlike; stems numerous, slender, scapiform or 1–3-furcate, the branches pedunculate or sometimes 2-headed, sparsely canescent-tomentulose; peduncles and involucre canescent-tomentulose; heads erect, small, about 40-flowered; involucre campanulate, about 6 mm high, 4 mm wide at middle in anthesis; outer bracts 5, about $\frac{1}{2}$ as long as the inner in anthesis, ovate, acute, glabrous, scarious, membranous-margined; inner bracts 8–9, ovate-lanceolate, acute, white-ciliate at tip, with a median dorsal row of rather strong setae which are purple or brown at the base and yellow above, glabrous on inner face (condition in fruiting heads not seen, but probably carinate and spongy-thickened); corolla 7–8 mm long; ligule 1 mm wide; teeth 0.2–0.4 mm long; corolla tube 2.5 mm long, glabrous; anther tube yellow, about 2.7×0.7 mm dis.; appendages 0.5 mm long, lanceolate, acute, united; filaments 0.3 mm longer; style branches 1.5 mm long, 0.1 mm wide, yellow; very young achenes 1.5 mm long, 0.4 mm wide, fusiform, strongly constricted below the expanded pappus disk, 10-striate, very finely spiculate (one partly mature achene was 2.5 mm long, greenish-purple, fusiform, shortly attenuate at apex); pappus white, 2.5 mm long, 1–2-seriate, very fine, soft, deciduous. Flowering May; flowers yellow.

Known only from the type locality.
Monomorphic.

Syria: environs of Hammah (= Hamah or Hama), 457 m, *Haradjian 1848*, in 1908 between Apr. 20 and May 4, spec. unic. (DL, fragments and photographs in UC).

It is possible that the plant reported by Koch (*Linnaea* 23[7] : 688. 1850) as *C. multiflora* S. et S. var *humilis, diffusa*, from the shore of the Caspian Sea, in Daghestan, belongs here. He cites *C. corymbosa* Ten. as a synonym; and he suggests that *C. parviflora* Desf. might be a small-flowered subspecies. Unfortunately, this specimen of Koch's has not been seen by me.

Relationship

Crepis insignis is very distinct in its relatively large rosette of caudical leaves and very short flower stems. Although the outer involucre bracts are like those of *C. vesicaria*, the inner bracts are very different, being glabrous on the inner face and having a dorsal median row of stoutish bicolored setae. Moreover, the mature achenes are probably not definitely beaked. It seems fairly safe to predict that in mature involucres the inner bracts are carinate and spongy-thickened. *C. insignis*, therefore, appears to belong in this section, and the involucre bracts resemble those of *C. parviflora*, except that in the latter species they are not bicolored. On the other hand, it is probable that the mature achenes of *C. insignis* are more like those of *C. neglecta*. In size of heads, florets, and flower parts *C. insignis* is very close to *C. parviflora* and *C. neglecta*; but in habit of the plant *C. insignis* shows most resemblance to *C. fuliginosa*.

164. *Crepis neglecta* L.

Mant. Pl., ed. 6 et Sp. Pl. ed. 2, 107. 1767. (Fig. 255.)

Annual, 1–5 dm high, mostly erect, corymbiform, sometimes low, diffuse (see m.v. 2, 3); root slender; caudical leaves up to 14 cm long, 3 cm wide, oblanceolate, rounded-obtuse, denticulate to pinnately parted, corneous-mucronate, gradually attenuate into a narrowly winged petiole, hispidulous with short pale glandless hairs; cauline leaves similar or sessile, or lanceolate, acute or acuminate, with broad amplexicaul acutely auriculate \pm lacinate base, uppermost, sometimes all, much reduced; stem branched above middle or beginning near base, or stems numerous, semidecumbent, corymbosely branched above, \pm hispidulous below, glabrescent above; branches slender, ultimate branchlets bent down just below heads before anthesis; peduncles 0.5–5 cm long, arcuate, very slender, not much thickened in fruit, tomentulose, pubescent or setulose near head; heads in anthesis erect, small, few or many-flowered; involucre cylindric-campanulate, 4–7 mm long, 1–4 mm wide at the swollen base in fruiting heads, ultimately reflexed; outer bracts few, small, linear, glabrous or pubescent; inner bracts 7–13, lanceolate, obtuse or acute, glabrous within, glabrous, tomentulose, or finely gland-pubescent without, rarely setulose near tip with greenish setalike hairs (see m.v. 1), ultimately carinate, spongy-thickened at base; receptacle alveolate-fimbriate, fimbriae low, membranous, very shortly and finely ciliate; corolla 5–8 mm long; ligule 1.25 mm wide, yellow with or without red on outer face; teeth 0.2–0.35 mm long; corolla tube about 2 mm long, densely pubescent with salient acicular hairs 0.05–0.4 mm long; anther tube 2.75×1 mm dis.; appendages 0.5 mm long, oblong, acute or obtuse; filaments 0.5 mm longer; style branches 1.5 mm long, 0.1 mm wide, green or yellow in certain variants; achenes pale brown, 2–2.5 mm long, fusiform, 10-ribbed, ribs spiculate, narrow with broader smooth spaces between, base narrow, hollow, calloused, apex \pm attenuate or very shortly beaked; marginal achenes seldom if ever beaked, some-

times ventrally compressed, 3-angled, paler; inner achenes sometimes more attenuate or very shortly beaked; pappus white, 2–3 mm long, 1-seriate, very fine, soft, caducous. Flowering April–July. Chromosomes, $2n = 8$.

Crepis striota Scop., Fl. Carn., ed. 2, 2: 99. 1772.

C. hyoseroides S. et S., Fl. Graec. Prod. 2: 139. t. 809. 1813.

C. oernua Ten., ex Rehb., Pl. Crit. 4: 5. t. 306. 1826 et Syll. Fl. Neap. 402. 1831.

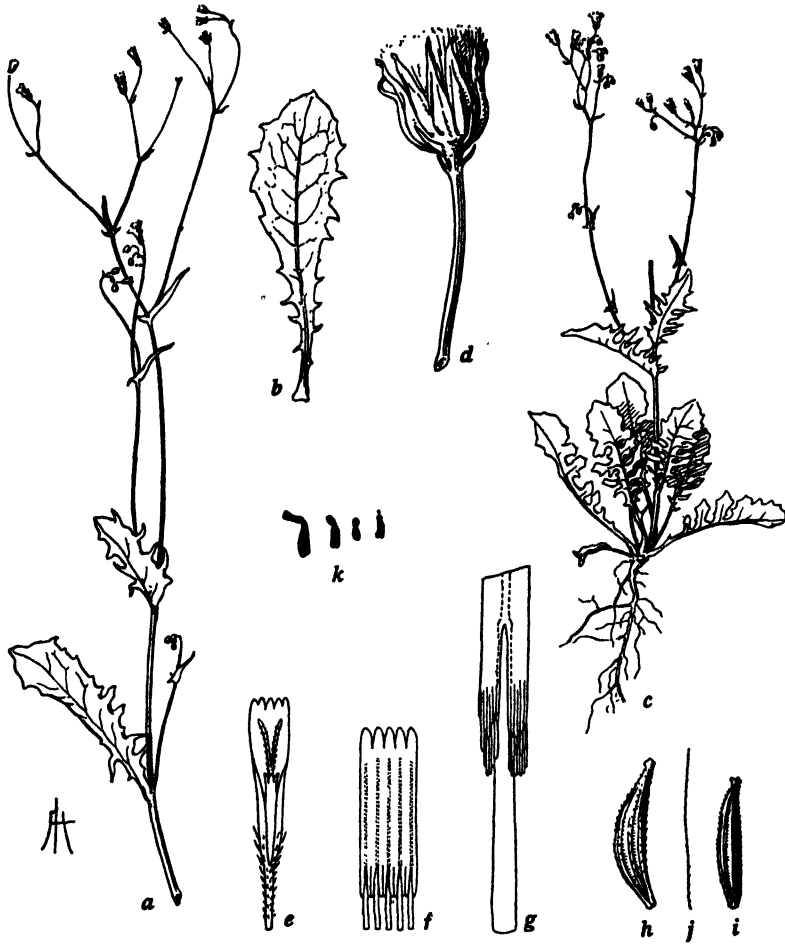


Fig. 255. *Crepis neglecta*, a, b, from type (L); c–j, from *Lacaita* 197/10 b (BML 12216); k, from hort. genet. Calif. 1753 (grown from seeds received from Marburg Bot. Gard.; cf. UC 676609): a, upper part of a plant, $\times \frac{1}{4}$; b, caudical leaf, $\times \frac{1}{4}$; c, plant, $\times \frac{1}{4}$; d, mature head, $\times 2$; e, floret lacking ovary, $\times 4$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h–j, marginal and inner achenes from different plants and a pappus seta, $\times 8$; k, somatic chromosomes, $n = 4$, $\times 1250$.

Barkhausia oernua Koch, Synops. 437. 1837.

C. polymorpha var. *striota* DC., Prod. 7: 162. 1838 in part.

† *C. corymbosa* Ten., ex Willk. et Lange, Prod. Fl. Hisp. 2: 249. 1870 ex descr.

Hieraciodes neglectum O. Kuntze, Gen. 1: 346. 1891.

Italy, from Calabria northward to the valley of the Po, eastward through Istria, S. Carniola, and Croatia into N. Greece, S. Bulgaria, Macedonia, Thrace, and N.W. Asia Minor. Adventive in the Tirol and S. Germany (acc. to Hegi) and probably in S. Spain.

Italy: locality uncertain (L) type (photo UC); Campania, Salerno, Majori, *Lacaita* 197/10, b (BML); Ravello, *Lacaita* in 1880 (BML) m.v. 1; Portici, *Heidreich* in 1843 (K, DS); Pompei, *Burnat et Cavillier* in 1907 (Bur); Naples, *Reynier* in 1813 (K); Latium near Rome, Tivoli, *Pellat* in 1903 (Grenoble); Tuscany, near Pisa, *Cessati, Caruel, et Savi* 531 (Po); Florence, *J. Ball* in 1848 (K); near Florence, *Groves* in 1876 (K, UC) m.v. 2; Tirol, Val Sugana, near S. Cristoforo, *Murz* in 1901 (UC); Istria, Trieste, *Tommadini* in 1851 (Ms, Bur); Pola, *Schultz* 88 (K). **Yugoslavia:** Fiume, *Noë* in 1837 (K); Montenegro, Gornji polje, Negusi, *Rohlena* in 1910 (BML) m.v. 2; Dalmatia, *Petter* (CA); Hercegovina, Mostar, Mt. Stolac, 200 m, *Raap* in 1895 (K, UC). **Bulgaria:** E. Rhodope Mts., Ortakjoi, near Bas Derman, *Achtarov* in 1932 (*vide* Stefanoff, in litt.) m.v. 1 (?). **Greece:** Sibthorp (Oxford-Druce) "*Crepis hyoseroides* ut videtur"; Thessaly, Kalampaka, *Sintenis* 246 (K, Bur); *ibid.*, between Kalampaka and Kastanea, along Penion R., *Babcock* 355 (UC); *ibid.*, foot of Mt. Zygos, Malakasi, *Miss Topali* 7 (UC) m.v. 3; Kato Lehonina, near Volos, *Miss Topali* in 1928 (UC) m.v. 1. **Asia Minor:** Smyrna, *Bornmüller* in 1906 (Weimar); Smyrna, *Fleischer* in 1827 (Mu). **Spain:** (adventive ?) Cadiz, between Sinea and Acompamento, *Porta et Rigo* 516 (Bur); Malaga, Cartama, *Reverchon* 252 (Bur).

Minor Variants of *C. neglecta*

1. Involucre \pm pubescent with glandless or glandular greenish hairs. In connection with the first specimen cited below, there is the following annotation: "This exactly tallies with the picture in Tenore's Flora, tab. 183-1." It happens that the specimens cited here have unusually long green hairs near the tips of the inner involucre bracts in some heads, and it is very doubtful whether in this respect these plants agree with Tenore's illustration. *Lacaita* in 1880 (BML), Ravello, Italy; *Lacaita* in 1880 (BML), Sambuco Road, Ravello, Italy; *Miss Topali* in 1928 (UC), Kato Lehonina, near Volos, Greece.

2. Low, often decumbent, slender; heads rather small. Plants mostly abnormal or mutilated from being trampled upon; most if not all ecads. *Groves* in 1876 (K, UC), between fields and on roads, near Florence, Italy; *Fiori et Beguinot* 1179 (Bur, BML), St. Gervasio, Florence, Italy; *Rohlena* in 1910 (BML), Negusi, Gornji polje, Montenegro.

3. Low, with several slender erect many-branched stems; heads rather small; style branches yellow. Perhaps a product of hybridization with *C. fuliginosa*. *Miss Topali* 7 (UC), Malakasi, foot of Mt. Zygos, N.W. Thessaly, Greece.

4. Low, decumbent, strongly resembling *C. fuliginosa* in habit and size of the plant, as well as in heads, florets, and achenes. Seeds from this plant produced (hort. genet. Calif. 3469b) progeny with $2n = 8$ chromosomes, like those of *C. neglecta*, except that one pair contained a translocated segment from *C. fuliginosa*. *Miss Topali* (UC 602788), south of Mt. Ossa, between Agyia and Selitsani, Thessaly, Greece.

Relationship

Crepis neglecta is closest to *C. corymbosa*, from which it is easily distinguished by the absence of long yellow setae on the involucre, except in certain glabrous forms of *C. corymbosa*, but always by the unbeaked marginal achenes, which are very similar to the inner achenes and are seldom retained by the inner involucre bracts. Furthermore, in *C. neglecta* the corolla is longer and relatively narrower, the anther tube is much longer, and the style branches are longer and usually green. It is probable that these two species overlap in S. Italy and that intermediate hybrid forms occur. It is close, also, to *C. fuliginosa* and *C. cretica*, from both of which it can usually be easily distinguished by the much larger size of the plant and all its parts, by the usually erect single stem as contrasted with the low diffuse habit of the other two species, and by the green style branches and less definitely beaked achenes, although *C. fuliginosa* is variable in respect to the last two characters. In N. Greece plants of *C. neglecta* are often suppressed by aridity or other features of the environment; but seeds taken from such plants in the wild have produced garden plants typical of *C. neglecta*, whereas in similar tests *C. fuliginosa* maintains its low diffuse habit and small size of plant and all parts. Field studies to determine the southern limit of distribution of *C. neglecta* in N. Greece would be of value in connection with the future history of the two species and their progeny. The fact that *C. neglecta* has 8 chromosomes, whereas *C. fuliginosa* has only 6, creates interesting possibilities from natural hybridization between the two (cf. Part I, p. 26).

In addition to the chromosomal differences between *C. neglecta* and its three closest relatives, *C. corymbosa*, *C. fuliginosa*, and *C. cretica*, the results of crossing experiments add further support to their recognition as valid species. It has been found to be difficult to obtain artificial hybrids between *C. neglecta* and either *C. fuliginosa* or *C. corymbosa*; also between *C. fuliginosa* and *C. cretica*. Furthermore, the F_1 hybrids between *C. neglecta* and *C. fuliginosa* were found by Tobgy (cf. *C. fuliginosa*) to be highly sterile; and any highly fertile F_2 progeny that could be obtained always resembled one or other of the parent species and had a chromosome complement characteristic of that species plus one chromosome from the other species. Obviously, further progenies would tend to revert to the pure species. Hence, these closest relatives of *C. neglecta* (cf. *C. fuliginosa*) may properly be considered as distinct species.

C. neglecta is a connecting species between its close relatives with beaked achenes, *C. corymbosa*, *C. apula*, *C. fuliginosa*, *C. cretica*, and *C. Suffreniana*, on one hand, and those with unbeaked achenes, *C. nicaeensis*, *C. capillaris*, *C. parviflora*, and *C. insignis*, on the other.

165. *Crepis corymbosa* Ten.

Cat., 1819; Syll. Fl. Neap. 401. 1831. (Fig. 256.)

Annual, mostly erect, paniculate-corymbiform, up to 4 dm high, sometimes low, diffuse (see m.v. 2); root slender; caudical leaves up to 17 cm long, 2 cm wide, oblanceolate, obtuse or acute, denticulate to pinnately parted, corneous-mucronate, gradually attenuate into a narrow petiole, hispidulous with short pale glandless hairs; lower cauline leaves similar, petiolate or sessile, middle cauline leaves lanceolate, acuminate, amplexicaul, auriculate, \pm lacinate, uppermost bractlike; stem paniculately branched from base upward or from base only and then divaricate or semidecumbent, \pm hispid with fine yellowish setae; branches slender, ultimate branchlets bent down just below heads before anthesis; peduncles 1–4 cm long, very slender, tomentulose, setulose or glabrescent; heads erect in anthesis and fruit, small, up to 50-flowered; involucre cylindric-campanulate, up to 6 mm long, 3.5 mm wide at the swollen base in fruiting heads, densely setose with yellow or greenish glandless setae, sometimes sparsely setose or glabrous, ultimately reflexed; outer bracts few, small, linear, acuminate; inner bracts 7–15, lanceolate, acute or obtuse, glabrous within, becoming navicular, spongy-thickened at base; receptacle alveolate-fimbriate, fimbriae low, membranous, very shortly and finely ciliate; corolla 6 mm long; ligule 1.5 mm wide, yellow, usually with red or outer face; teeth 0.15–0.25 mm long; corolla tube 2 mm long, barbellulate with papilliform hairs, 0.05 mm long, and base of ligule pubescent with acicular hairs up to 0.5 mm long; anther tube 2×0.9 mm dis.; appendages 0.5 mm long, oblong, acute; filaments 0.3 mm longer; style branches 1 mm long, 0.1 mm wide, yellow; achenes pale brown, 2–2.75 mm long; marginal achenes laterally compressed, dorsally curved, ventrally straight, flattened, paler and 3-angled, strongly attenuate below summit or definitely beaked, strongly barbed, often retained by involucre bracts; inner achenes fusiform, narrowed at the strongly calloused base, strongly attenuate into a beak less than 1 mm long, 10-ribbed, ribs strongly spiculate; pappus white, 2.5–3.5 mm long, 1-seriate, very fine, soft, caducous. Flowering Apr.–June. Chromosomes, $2n = 8$.

S. Italy from Calabria northward to S. Campania and eastward to Puglia (Apulia); Greece, in Corfu and Cephalonia; littoral to low montane.

Authentic specimens of Tenore are cited below.

Italy: Calabria, Reggio, Cinquefronde, near Mt. Limina, *Lacaita* 74/07 (BML) partly m.v. 1; Naples (†) *Tenore dedit* 1824 (K); *ibid.*, † *Tenore misit* 1814 (DC, UCf); *ibid.*, † labeled var. *humilis* Ten. (DC) m.v. 2; Puglia (Apulia), Taranto, Serrone de Leucaspidi, *Fiori et Béguinot*

1179b (Bur, G, BML); Puglia, Gargano Mts., Mt. S. Angelo, *Porta et Rigo* in 1874 (Bur); Gargano Mts., near Mt. S. Angelo, *Porta et Rigo* 197 (BML). Greece: Corfu, *Miss Topali* in 1931 (UC); Ins. Corcyra (Corfu), *J. Ball* in 1877 (K); Cephalonia, lower reg. of Mt. Aeni (Monte-nero), Omalo Valley, near Gerasemus Monastery and Francata village, *Heldreich 3560* (K) m.v. 1.

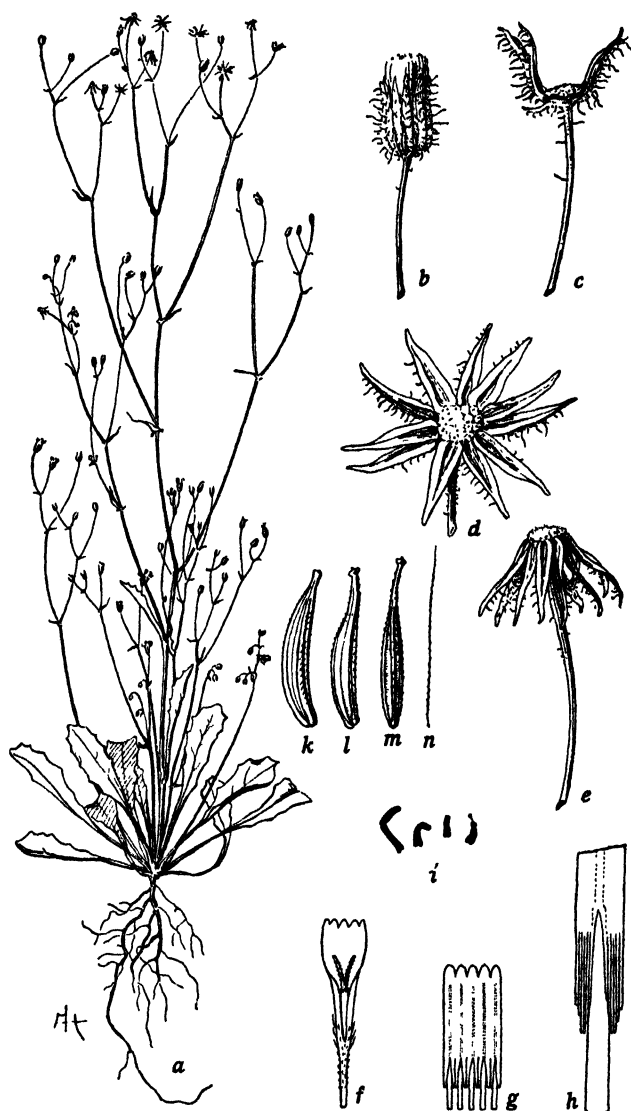


Fig. 256. *Crepis corymbosa*, from Miss S. P. Topali in 1931 (UC 506842, 463907): a, plant, $\times \frac{1}{4}$; b-e, heads, $\times 2$; f, floret lacking ovary, $\times 4$; g, anther tube, $\times 8$; h, detail of appendages, $\times 32$; i, somatic chromosomes, $n = 4$, $\times 1250$; k-n, 2 marginal achenes and an inner achene and pappus seta, $\times 8$.

Minor Variants of *C. corymbosa*

1. Involucre glabrous. *Lacaita 74/07* (BML), near Mt. Limina, Cinquefronde, Reggio, Calabria, Italy; *Heldreich 3560* (K), near Gerasemus Monastery and Francata village, Omalo Valley, lower part of Mt. Aeni (Monte-nero), about 600 m, Cephalonia, Greece.

2. (*C. corymbosa* var. *humilis* Ten., loc. cit.) Low, diffuse, very slender. *Tenore* (DC), without locality, probably Italy; *Lacaita* in 1880 (BML), "forming a yellow carpet on the stony serrone," Leucaspide, Taranto, Italy.

Relationship

C. corymbosa is closest to *C. neglecta*, from which it is distinguished by the usually dense yellowish setae on the involucre (except m.v. 1), by the somewhat smaller heads and more prominent pappus, by the more definitely modified marginal achenes which tend to be retained in the inner bracts of the involucre, by the usually more slender and definitely beaked inner achenes, the shorter florets and relatively wider ligules, shorter anther tube and anther appendages, and the shorter, yellow style branches. It is close, also, to *C. fuliginosa* and *C. cretica*, from both of which, at least in its typical forms, it is clearly distinguished by the more robust, erect, hispidulous stem and the yellow setae of the involucre on mature heads, and always by the laterally compressed, ventrally pale marginal achenes. In N.W. Greece or the adjacent islands it may meet and hybridize with *C. fuliginosa*, giving rise to intermediate forms which would be very difficult to classify. The fact, however, that *C. corymbosa* has 8 chromosomes, whereas *C. fuliginosa* has 6, would probably cause high sterility in such hybrids, which, unless a fertile amphidiploid hybrid should arise and prove a successful competitor, would tend to preserve the present species. *C. corymbosa* is less close to *C. Suffreniana* and *C. apula*, although it has been confused with the former.

166. *Crepis fuliginosa* Sibth. et Sm.

Fl. Graec. Prod. 2: 138. 1813. (Fig. 257.)

Annual, low, diffusely branched from base or sometimes erect, slender; root slender; caudical leaves few or numerous, 2–6 (8) cm long, 1–2 cm wide, oblanceolate, obtuse, denticulate to pinnately parted with 4–6 pairs of lateral segments, corneous-mucronate, gradually attenuate into a winged petiole, hispidulous with short pale glandless hairs; cauline leaves similar or lanceolate, acuminate, sessile, amplexicaul, lacinate, mostly very small; stems mostly numerous, slender, semidecumbent, remotely branched, branches slender, corymbiform, bent down just below heads before anthesis, hispidulous below, glabrous above; peduncles 0.5–5 (7) cm long, very slender, not much thickened in fruit, glabrous or pubescent near head; heads erect in anthesis, small, (30–40–) 50-flowered; involucre campanulate, 3.5–5.5 mm long, 2–3.5 mm wide at the swollen base in fruiting heads, glabrescent, tomentulose, shortly gland-pubescent with fine black hairs and glands or \pm setuliferous with very fine green glandless hairs, ultimately reflexed; outer bracts few, minute, linear; inner bracts mostly 8, lanceolate, acute, glabrous within, becoming carinate, spongy-thickened at base; receptacle areolate-fimbriate, fimbriae obscure, naked or minutely ciliate; corolla about 5 mm long; ligule 1–1.3 mm wide, yellow with red on outer face, pubescent at the base with acicular hairs up to 0.4 mm long; teeth 0.15–0.4 mm long; corolla tube about 1.5 mm long, minutely barbel-lulate with papilliform hairs 0.02–0.1 mm long; anther tube about 2×0.8 mm dis.; appendages 0.4–0.5 mm long, lanceolate, acute, very thin, transparent; filaments 0.4 mm longer; style branches 1 mm long, 0.1 mm wide, yellow or sometimes green; achenes pale brown, 1.75–3.25 mm long, fusiform, usually beaked (cf. m.v. 3), the beak sometimes very short, often $\frac{1}{4}$ – $\frac{1}{3}$ of the whole achene, rarely longer (cf. m.v. 1), 10-ribbed, ribs spiculate; marginal achenes ventrally \pm compressed and 3-angled, otherwise similar to inner achenes; pappus white, sometimes with a purplish luster, 2–3 mm long, 1-seriate, very fine, soft, caducous. Flowering April–June. Chromosomes, $2n = 6$.

Crepis neglecta f. *graecca* Vierh., Verhandl. Zoöl.-Bot. Ges. Wien, 1914: 263.

S. Greece, the whole Peloponnesus including Cerigo (Cythera) I., Attica, E. Thessaly, Cyclades (and probably other Aegean and Ionian Islands), and in Palestine (adventive ?). The northern limit of this subspecies has not been definitely



Fig. 257. *Crepis fuliginosa*, a-j, from Costopulos in 1931 (UC 506841); k-t, from Guiol in 1930 (UC 429484); u-z', from Forsyth Major 824 (RB): a, plant, $\times \frac{1}{4}$; a', somatic chromosomes, $n = 3$, $\times 1250$; b-d, 3 heads, $\times 2$; e, floret lacking ovary, $\times 4$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h-j, 2 achenes and a pappus seta, $\times 8$; k, plant, $\times \frac{1}{4}$; l, m, 2 heads, $\times 2$; n, floret lacking ovary, $\times 4$; n', detail of ligule teeth, $\times 50$; o, anther tube, $\times 8$; p, detail of appendages, $\times 32$; q, old head, $\times 2$; r-t, 2 achenes and a pappus seta, $\times 8$; u, head, $\times 2$; v, inner involucre bract, $\times 4$; w, floret lacking ovary, $\times 4$; x, anther tube, $\times 8$; y, detail of appendages, $\times 32$; z, z', achene and pappus seta, $\times 8$.

determined, but in the N. Peloponnesus there are indications of overlapping and hybridization with *C. neglecta* (cf. Miss S. P. Topali's plant from Patras and Zuccarini's plant from Old Corinth, cited below). Notable among these indications are a tendency to more erect habit, more leafy stems, and dark green style branches.

Field studies to the north of the Gulf of Patras and the Gulf of Corinth are needed in order to determine the southern limits of *C. neglecta*. The specimens of Miss Topali, from the Pelion—Mt. Ossa district in E. Thessaly prove that this species is well established in that region. If the species is adventive in Thessaly, as seems likely, Trikeri may have been the point of entry. One of Miss Topali's specimens from Agyia, near Mt. Ossa, is of special interest because cytological study of progeny grown from it indicates that it is of hybrid origin and that the other species involved is *C. neglecta* (see m.v. 5). The reported occurrence of this species on the Athos Peninsula by Turrill (Bull. Misc. Inf. Kew, 1937 [4]: 246) may indicate a still wider, earlier distribution; but it seems more likely that the plant was introduced here, as well as in Thessaly, from S. Greece. The station is described as: "Between Pyrgos and Xerxes Canal, on bare stony ground." The specimen, no. 2449, has not been seen by me.

Although the type was not seen by me, the careful work of Vierhapper (Verhandl. Zool.-Bot. Ges. Wien, 1914: 265–269) with citation of specimens leaves no doubt concerning the identity of this species.

Greece: Peloponnesus; Cerigo I. (Cythera), Milapotamo, *Miss Topali* in 1933 (UC); Cerigo I., Trevelyan in 1842 (Oxford-Druce); Laconia, route from Tripoli to Sparta, 600–900 m, *Babcock 325* (UC); Laconia, trail from village near Sparta to Taygetus (Pentodaktylon) Mts., about 1200 m, *Babcock 329* (UC) m.v. 3; Laconia, Taygetus Mts., Mt. St. Elias, near summit, "Megala Zonaria," about 2000 m, *Babcock 332* (UC); Laconia, near Gytheion, castle of Passavan, *Miss Topali* in 1933 (UC); N.W. Laconia, Mt. Selitza reg., near Kalamata, Zahn 1353 (K); Arcadia, Kerpini, near Kalavryta, *Costopulos* in 1931 (UC); Arcadia, near Makryisia, *Lacaita* in 1883 (BML); Arcadia, Megaspelacon, about 940 m, *Costopulos* in 1931 (UC); Achaia, Patras, *Miss Topali* in 1931 (UC) m.v. 4 p.p.; Corinthia, Akro-Kornithos, *Haussknecht* in 1885 (K); Argolis, *Sprunner* (Mo); Argolis, Hydra I., *Guiol* in 1930 (UC); Argolis, Kassos, near Argos, *Forsyth Major 824* (RB) m.v. 1; Attica, near Heracleon, *Heldreich 520* (K); Attica, Mt. Parnes, *Guiol* in 1930 (UC); Attica, Pentelikon Mts., *Guiol* in 1930 (UC); Aegean Is., Cyclades, Syra, *Gandoger* in 1919 (K); Cyclades, Teni, *Heldreich* (K); E. Thessaly, Pelion, Megneria Pen., Trikeri, *Miss Topali* in 1937 (UC) $2n = 6$; E. Thessaly, Larissa, south of Mt. Ossa, Agyia, *Miss Topali* in 1937 (UC) m.v. 5. **Palestine:** Jerusalem, *Miss Topali* in 1931 (UC) probably adventive.

Minor Variants of *C. fuliginosa*

1. Achenes pale purplish-brown, yellowish at apex, subcompressed, with narrow beak $\frac{1}{2}$ as long as whole achene; pappus whitish with a distinct purplish luster; involucre 6 mm high, finely gland-pubescent, \pm purplish; corolla 5.5 mm long; ligule 1 mm wide; teeth 0.2–0.3 mm long; corolla tube 1.75 mm long, pubescent with papilliform or acicular hairs 0.05–0.15 mm long, and base of ligule with hairs up to 0.35 mm long; anther tube 2.75×0.9 mm dis.; appendages 0.5 mm long, lanceolate, acute, very thin, transparent; filaments 0.4 mm longer; style branches 1 mm long, 0.1 mm wide, yellow. This is the only form known to the writer in which the achenes have a beak as long as the body of the achene, which serves to focus attention on the pronounced tendency of this species to have beaked achenes. (Fig. 257, *u-s*.) *Forsyth Major 824* (RB, UC), among rocks, Kassos, near Argos, Greece.

2. (*C. fuliginosa* var. *adscendens* S. et S., loc. cit.) Of doubtful identity. The specimens cited below may be forms of this species or hybrids between it and either *C. corymbosa* or *C. neglecta*. *Margot* in 1837 (DC VII: 167, n. 7), Zante I.; *Sibthorp 170* (Oxford-Druce), Zante I.

3. Plant erect, 1.5–3 dm high; caudal leaves few, cauline leaves gradually reduced, uppermost bractlike; stem 0.75–1.5 mm wide near base, terete, finely gland-pubescent, remotely branched from base upward, few-headed; peduncles, bracts, and involucre finely gland-pubescent with short and long green or black hairs; style branches pale green; achenes 1.75–2 mm long, 0.5 mm wide, not beaked, alternate ribs stronger. Other plants in the same population were more nearly typical in habit, and garden progeny were quite typical. The progeny of certain plants in the population had $2n = 6$ chromosomes. It is probable that these erect taller plants are ecads induced by the partially shaded situation. *Babcock 329* (UC), among firs on moist banks near a spring, about 1200 m, trail from village near Sparta to summit of Taygetus Mts., Laconia, Greece.

4. Habit like that in m.v. 3; plant 2.5 dm high, slender; caudal leaves spatulate, denticulate, long-petiolate; stem few-branched, few-headed, glabrescent; involucre very shortly gland-pubescent; style branches pale green; achenes shortly beaked. Since it grew near plants of typical

habit, this is probably another shade form; but one of these plants had dark green style branches, and another had larger caudical leaves than is usual in this species, resembling those of *C. neglecta*. It is possible that some of the variations in this population were the result of hybridization with *C. neglecta*, yet it is equally possible that they were merely manifestations of the variability which has already been noted to be characteristic of this species. *Miss Topali* in 1931 (UC), Patras, Greece.

5. Habit like that in m.v. 3; plant 3 dm high; caudical leaves few, cauline leaves gradually reduced, uppermost bractlike; stem 1.5 mm wide at base, terete, densely pubescent below with appressed pale mostly glandless hairs, sparsely setulose above with white spreading glandless setules, remotely and shortly branched from near base upward, few-headed; peduncles very fine, glabrous or slightly setulose near base; heads very small; involucre 4 mm high, 2.5 mm wide at middle, glabrous; inner bracts 8-9; corolla 5-6 mm long; style branches yellow; achenes 2 mm long, 0.3-0.4 mm wide, both marginal and inner ones shortly beaked. Cultivated progeny of the one plant collected in the wild had $2n = 9, 10$, and 11 chromosomes, none of which can be assigned with certainty to *C. fuliginosa*, whereas the longest pair appears to have come from *C. neglecta*. Evidently this form is a complex hybrid derived from *C. neglecta* \times *C. fuliginosa*, although superficially it greatly resembles the shade form collected by the author on Mt. Taygetus (m.v. 3). Further collections and field studies in E. Thessaly, especially in the vicinity of Mt. Ossa, would be of interest. *Miss Topali* in 1937 (UC), Agyia, south of Mt. Ossa, E. Thessaly, Greece.

Relationship

Crepis fuliginosa is closest to *C. cretica*, which it resembles in habit but from which it is distinguished by being more robust, by having fewer lateral segments of the caudical leaves, and by having larger heads and broader achenes. In length of achenes and length of beak *C. fuliginosa* is much more variable than *C. cretica*, but in the latter the achenes are more slender and delicate. It is not unlikely that *C. fuliginosa* is occasionally adventive in Crete, and vice versa with respect to *C. cretica*, but, since *C. fuliginosa* has six chromosomes and *C. cretica* eight, the F_1 hybrids would probably be highly sterile, a situation which would tend to preserve the present species.

Crepis fuliginosa is also close to *C. neglecta* and *C. corymbosa* and probably hybridizes with both species where they overlap with it, but here again the difference in chromosome number would tend to preserve all three. Experimental crosses between *C. fuliginosa* and *C. neglecta* have produced only hybrids with very low fertility; and certain wild plants suspected of being natural hybrids between these species produced progeny which were highly sterile. At the same time, the possibility must be recognized that, through backcrossing of F_1 hybrids with the parent species, fertile hybrid derivatives might be produced and might give rise to local races, combining the characters of the parent species, but differing from both in their chromosome morphology. Just such a form seems to have been discovered by *Miss Topali* in her collection from near Mt. Ossa in E. Thessaly. Nevertheless, the investigations of Tobgy on artificial hybrids between these two species have shown that, even though some of the F_2 and backcross hybrids are highly fertile, they all have a complete *C. fuliginosa* or *C. neglecta* complement of chromosomes plus one chromosome from the other species. The F_3 progeny of such plants have not yet been studied, but it is safe to predict that the foreign chromosome will tend to be eliminated, leaving only plants of one or the other species, together with occasional intergrades resulting from interchange of segments through crossing over. Such an intergrade was discovered among *Miss Topali's* plants from the Mt. Ossa district (cf. *C. neglecta*, m.v. 4).

There is every reason to believe that these four species (*C. neglecta*, *C. corymbosa*, *C. fuliginosa*, and *C. cretica*) arose from a common ancestral stock at a time antecedent to their present geographical isolation. It is highly probable, therefore, that they possess a common residual genic complement, even though they differ

considerably in their chromosomes. The problem of the origin of *C. fuliginosa* in particular is an extremely interesting one. The hypothesis that it came from an 8-chromosome ancestor, either *C. neglecta* or a common ancestor of the two, is in harmony with much other evidence on the evolution of *Crepis* species. The greater reduction in size, the marked variability, and the restricted distribution of *C. fuliginosa* indicate that it is of more recent origin than *C. neglecta*. This hypothesis has been practically proved by Tobgy. His study of meiosis in the highly sterile F_1 hybrids revealed the existence of homologous segments in the chromosomes of the two species. He concludes that the A and D chromosomes of *C. neglecta*, through unequal reciprocal translocation, gave rise to the A and D chromosomes of *C. fuliginosa*, whereas the B and C of *C. neglecta*, through a similar interchange of segments, gave rise to the B chromosome of *C. fuliginosa*. One arm of the C chromosome of *C. neglecta* and its centromere are absent from the complement of *C. fuliginosa*. The original mutations which gave rise to the chromosome complement of *C. fuliginosa* presumably occurred in the common ancestor of the two species (see Part I, pp. 26, 148).

167. *Crepis cretica* Boiss.

Diag. Pl. Or. Nov., ser. 1, 11: 53. 1849. (Fig. 258.)

Annual, low, diffusely branched from the base; root very slender; caudical leaves rarely up to 7 cm long, 0.5–1.5 cm wide, narrowly oblanceolate, obtuse or acute, dentate to pinnately parted, with 6–10 pairs of lateral segments, corneous-mucronate, gradually attenuate into a winged petiole, hispidulous with short pale glandless hairs; cauline leaves similar or lanceolate, acuminate, sessile, amplexicaul, auriculate, \pm lacinate, uppermost bractlike; stems numerous, very slender, decumbent, few-branched, branches elongated, 1–4-headed, hispidulous or gland-pubescent near base or glabrescent, ultimate branchlets bent down just below heads before anthesis; peduncles 1–6.5 cm long, filamentous, glabrous or pubescent near head; heads erect, very small, 30–40-flowered; involucre campanulate, 3–5.5 mm long, 1.5–3.5 mm wide at the swollen base in fruiting heads, glabrous, tomentulose or minutely gland-pubescent or sometimes with longer glandless hairs, ultimately reflexed; outer bracts 4–5, very narrow; inner bracts mostly 8, lanceolate, acute, glabrous within, becoming carinate, spongy-thickened at base; receptacle areolate, subfimbriate, fimbriae obscure, naked or minutely ciliate; corolla 5.5 mm long; ligule 1.5 mm wide; ligule teeth 0.2–0.7 mm long, deep purple in marginal florets; corolla tube 1.5 mm long, pubescent with papilliform acicular hairs 0.05–0.35 mm long; anther tube 2×0.9 mm dis.; appendages 0.4–0.5 mm long, lanceolate, acute or acuminate, very thin, transparent; filaments 0.3 mm longer; style branches about 1 mm long, 0.1 mm wide, yellow; achenes 2 mm long, 0.3 mm wide, very delicate, fusiform, base narrow, calloused, 10-ribbed, ribs narrow, spiculate, beak short, fine; pappus white, 1.5–2 mm long, very fine, fugacious. Flowering March–June. Chromosomes, $2n = 8$.

Crepis bellidifolia Noë, ex Nyman, Consp. 460. 1854–1855.

Hieraciodes creticum O. Kuntze, Gen. 1: 345. 1891.

Crete (and Scarpanto [Karpathos], acc. to Vierhapper, Oesterr. Bot. Zeitschr. 65: 71–73. 1915). Generally distributed in lower and middle altitudes in Crete; in many places common.

Monomorphic, except ecological variants.

Crete: without locality, *Raulin 368* (Bo, UCf) type; *Malaxa* dist., *Reverchon* in 1883 (Bo, CP); *Kisamo* reg., *Reverchon* in 1884 (Bur, BML, UCf); *Canea* reg., *Gandoger* in 1914 (Mo); *Canea* reg., *St. Theodoras I.*, *Gandoger* in 1914 (Mo); *Madaras* Mts., trail from Askifou to Omalo

Plateau, *Babcock 302* (UC); Samaria Gorge, St. Nicholas Chapel, *Babcock 318* (UC); Imbros Gorge, *Babcock 299* (UC); Rethymno dist., Retimo, *Sieber* (B) as *C. nemausensis*; Candia reg., Mt. Strombolo, *Gandoger* in 1915 (K) m.v. 1; Sitia Mts., Toplou, *Gandoger* in 1914 (Mo); Tybaki dist., *Eberstaller* in 1914 (UWG); Klima-Tybaki, *Wettstein* in 1914 (UWG, UCf).

Minor Variant of C. cretica

1. Very slender erect plants, 0.8–1 dm high; stems 1 or 2, branched above, 2–4-headed. Probably a reduced form, caused by crowding. *Gandoger* in 1915 (K), Mt. Strombolo, Candia reg., Crete.

Relationship

Crepis cretica is closest to *C. fuliginosa*, which it resembles in habit but from which it is distinguished by the less robust, often decumbent stems, filamentous peduncles, and smaller heads, the narrow caudical leaves with more numerous

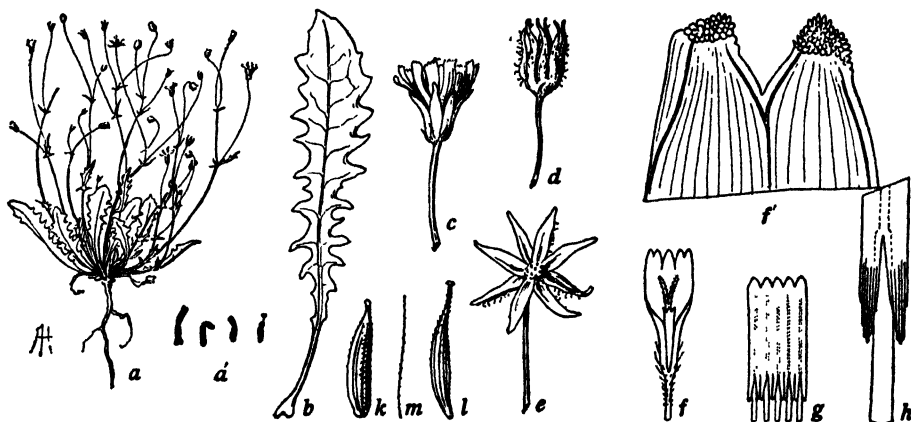


Fig. 258. *Crepis cretica*, from *Babcock 299, 302*, and *318* (UC 429376, 506832): *a*, plant, $\times \frac{1}{4}$; *a'*, somatic chromosomes, $n = 4$, $\times 1250$; *b*, basal leaf, $\times 1$; *c-e*, heads, $\times 2$; *f*, floret lacking ovary, $\times 4$; *f'*, detail of ligule teeth, $\times 50$; *g*, anther tube, $\times 8$; *h*, detail of appendages, $\times 32$; *k-m*, marginal and inner achenes and a pappus seta, $\times 32$.

lateral segments, and the very slender, delicate achenes. It is close also to *C. neglecta* and *C. corymbosa*, but very distinct from them, although probably derived from the former or a common ancestor before the present geographical isolation of the species (see *C. fuliginosa* and Part I, p. 148).

168. *Crepis apula* (Fiori) Babe.

Univ. Calif. Publ. Bot. 19: 399. 1941. (Fig. 259.)

Annual, 0.5–3.5 dm high; caudical leaves 2–9 cm long, 0.6–1.8 cm wide, oblanceolate, obtuse or acute, denticulate, dentate or runcinate-pinnatifid, with close rounded lateral segments, attenuate into a short, sometimes broadly winged petiole, pubescent, with very short spreading yellow glandless hairs or glabrous; cauline leaves lanceolate, acute or acuminate, sessile, subamplexicaul, acutely dentate or nearly entire, auriculate; stem robust, erect, remotely branched from near base upwards, lower branches nearly as long as axis, somewhat spreading, cymosely few- or many-headed, sulcate or striate, densely hispid with long yellow glandless setae; peduncles 0.5–4 cm long, arcuate, rather stout, gland-pubescent with fine hairs and small black glands; heads nodding before anthesis, small, 35–45-flowered; involucre cylindric-turbinate, 6–8 mm high, 3–4 mm wide near base; outer bracts 10, unequal, longest $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner, lance-linear, acute, white-ciliate at tip, like peduncle and inner bracts, canescent-tomentulose and pubescent with dark gland hairs; inner bracts 10–14, lanceolate, acute, white-ciliate at tip, becoming rounded-carinate

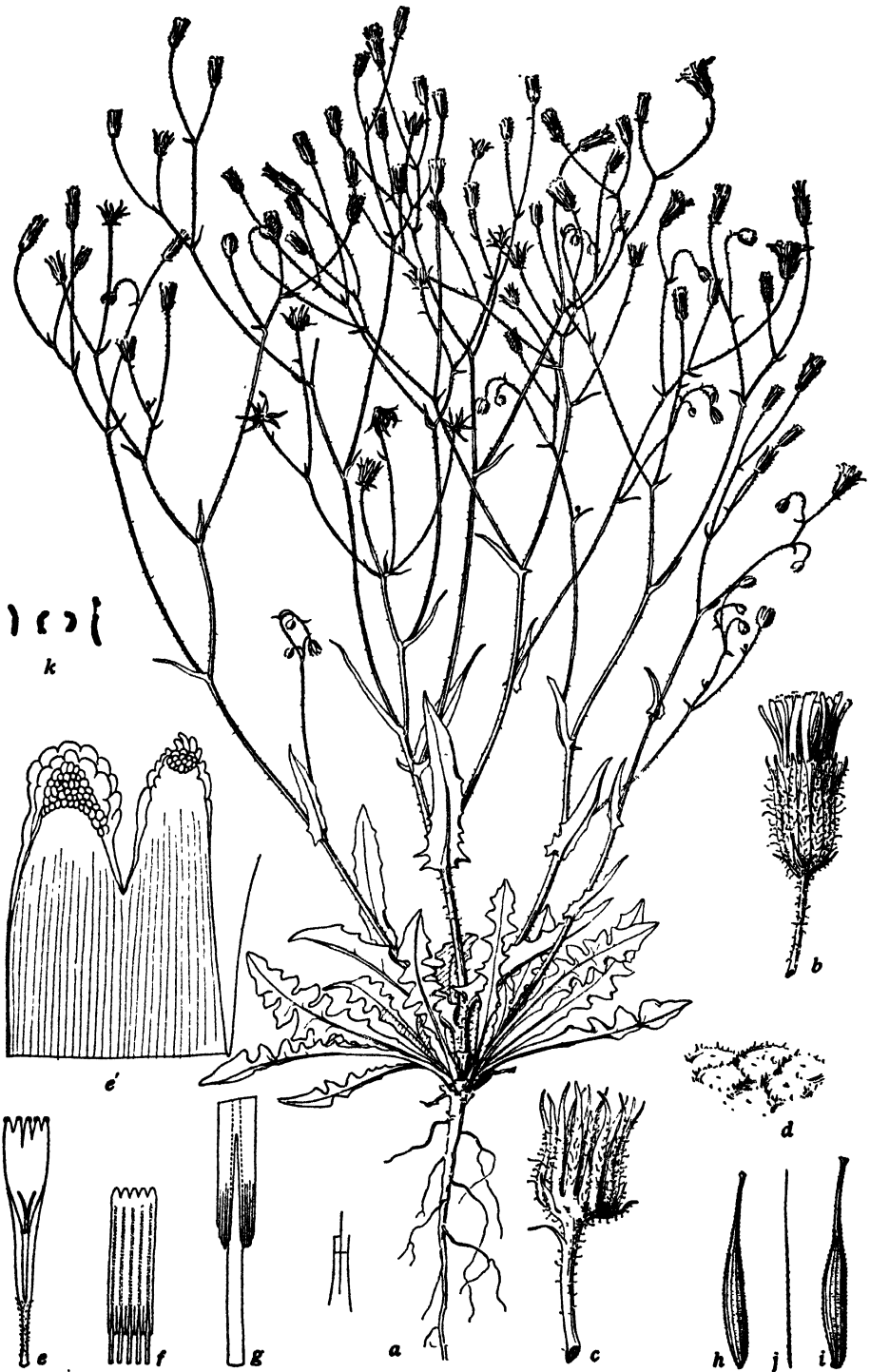


Fig. 259. *Crepis apula*, from Locaita in 1910 (BML 12192, 12421); *k*, from hort. genet. Calif. 3474 (grown from seeds collected in Calabria, Italy, by Dr. J. Bornmüller; cf. UC 534150): *a*, plant, $\times \frac{1}{2}$; *b*, head, $\times 4$; *c*, fruiting head, $\times 4$; *d*, detail of receptacle, $\times 25$; *e*, floret lacking ovary, $\times 4$; *f*, detail of ligule teeth, $\times 50$; *g*, anther tube, $\times 8$; *h*, detail of appendages, $\times 32$; *h-j*, 2 achenes and a pappus seta, $\times 8$; *k*, somatic chromosomes, $n = 4$, $\times 1250$.

and spongy-thickened, glabrous within; receptacle areolate, shortly and finely ciliate; corolla 8.5 mm long; ligule 1.5 mm wide; ligule teeth 0.2–0.6 mm long; corolla tube 2 mm long, very slender, densely pubescent with minute curved hairs; anther tube 2.5×0.75 mm dis.; appendages 0.5 mm long, oblong; filaments 0.5 mm longer; style branches 1 mm long, 0.1 mm wide, yellow; achenes very dark brown or nearly black, 3–3.5 mm long, straight and subterete or slightly curved and flattened on one side, constricted above the narrow very finely calloused hollow base, abruptly attenuate into a fine beak 1–1.5 mm long, with white expanded pappus disk, 10-ribbed, ribs narrow, rounded, finely spiculate to the very base under lens; pappus white, 3.5 mm long, 1-seriate, very fine, soft, caducous. Flowering, acc. to elevation, Mar.–June; flowers yellow, purplish on outer face of ligules.

Crepis Suffreniana var. *apula* Fiori, ex Fiori, Paol. et Bég., Fl. Anal. d'Ital. 3: 433. 1904.

Italy, in Puglia. The name of this species is a contraction of Apulia or Appulia, the Latin for Puglia, the southeasternmost province of Italy. All of the collections known to the present author were made at low elevations near Taranto, except one, at La Sila, Calabria, the southernmost province of Italy. This last, which came from an elevation of 1000 m, is of special interest because it throws doubt on Fiori's report that *C. Suffreniana* occurs in Calabria, since *C. apula* was confused by him with *C. Suffreniana*. Also, this collection indicates that *C. apula* occurs from littoral to submontane elevations; and, since *C. corymbosa* is similarly distributed in the same region, it would seem likely that the two species might hybridize naturally. They are, however, reported by Lacaita to occur together at Leucaspide near Taranto; and, among the specimens from that station examined by me, there has been no good evidence of intergradation between the two species. Lacaita's observation (in herb.), that *C. apula* is more precocious in flowering, may indicate that when the two occur together the flowering periods do not overlap. Further collections, with field studies, examination of the chromosomes, and hybridization experiments, would be of value. For the present it may be assumed that the two species are physiologically isolated.

Monomorphic.

Italy: Puglia, Lecce Prov., Taranto, Pineta del Pantano, sandy places near the sea, *Lacaita* in 1910 (type BML, UCf, Bur, G, Fl, all Fiori et Béguinot, Ital. Exsic. II, 1394); Taranto, Pineta del Pantano, *Lacaita* in 1910 (BML); near Taranto, Leucaspide, turf on stony ground, *Lacaita* in 1880 (BML); near Taranto, Leucaspide, gravelly bottom of gravina, with *C. corymbosa*, *Lacaita* in 1881 (BML).

Relationship

Crepis apula is closest to *C. Suffreniana* and *C. corymbosa*, from both of which, as first observed by Lacaita (see critical notes in Herb. Brit. Mus., Lacaita's folio no. 2944) it differs in the following points: (1) stem very hispid below; (2) caudical leaves differ in form; (3) peduncles rather robust, gland-hairy; (4) involucre gland-hairy; (5) achenes longer beaked; (6) inner bracts of fruiting heads neither straight, as in *C. Suffreniana*, nor incurved enclosing marginal achenes, as in *C. corymbosa*; (7) more precocious in flowering. To these may be added the more robust habit, larger heads, much longer florets and anther tubes, and the nearly black achenes with ribs minutely barbed to the base of the fruit. Hence, this species is morphologically, and probably physiologically, distinct from its nearest relatives. It also appears to be very constant except for variability in size of the plants under different environmental conditions.

169. *Crepis Suffreniana* (DC.) Lloyd

Fl. Loir. Inf. 155. 1844. (Fig. 260.)

Slender annual, 0.3–3 dm high; basal leaves 0.7–5 cm long, 3–12 mm wide, spatulate or oblanceolate, obtuse or acute, denticulate, dentate or runcinate-pinnatifid, attenuate into a narrow petiole, finely hispidulous on both sides; cauline leaves sessile, lanceolate, acute, subamplexicaul, acutely auriculate; stem erect, cymosely branched above or from near base, the branches few-headed, or stems several, erect or ascending, few-headed, \pm hispidulous below with very short fine yellow glandless hairs, glabrous above; peduncles 0.5–5 cm long, very slender, glabrous or canescent-tomentulose; heads erect or nodding before anthesis, small, few- or many-flowered; involucre in mature heads 4–6 mm high, 2–3 mm wide near base; outer bracts about 12, nearly equal, $\frac{1}{4}$ – $\frac{1}{3}$ as long as inner bracts, linear, acute; inner bracts 10–16, lanceolate, acute, membranous-margined, becoming dorsally keeled and spongy-thickened, canescent-tomentulose and finely setulose with dark green glandless setules, glabrous on inner face; receptacle areolate, very shortly and finely ciliate between areoles; corolla 5 mm long; ligule 0.65 mm wide; teeth 0.05–0.15 mm long; corolla tube 2 mm long, very slender, beset with spreading acicular hairs 0.05 mm long; anther tube 1×0.5 mm dis.; appendages 0.4 mm long, narrow, acute; filaments 0.25 mm longer; style branches 0.5 mm long, 0.1 mm wide, yellow, apiculate, unilaterally alate, the wing membranous; achenes deep purplish-brown, 3–4 mm long, 0.3–0.4 mm wide, straight and subterete or slightly curved and flattened ventrally, constricted above the narrow yellow-calloused hollow base, abruptly attenuate into a fine beak about 1 mm long, with expanded white pappus disk, 10 ribbed, ribs narrow, rounded, smooth, beak finely spiculate; pappus white, 2.5–3 mm long, 1-seriate, very fine, soft, deciduous or semipersistent. Flowering May–June; flowers yellow with deep purplish-red on outer face of ligules. Chromosomes, $2n = 8$.

Crepis bellidifolia var. β Lois., Fl. Gall. 2: 195. 1806–1807, *fide* Gr. et Godr., Fl. Fr. 2: 333. 1848–1856.

Hieraciodes Suffrenianum O. Kuntze, Gen. 1: 346. 1891.

Maritime districts of S.W. and S.E. France, often on sandy soil; near Pisa, Italy, where, acc. to Fiori, it may have been introduced. But Fiori's confusion of this species with *C. apula* (q.v.) makes his report that *C. Suffreniana* occurs in S. Italy (Calabria) very doubtful. This doubt is further increased by the recent collection of *C. apula* in Calabria by Bornmüller. A photograph of the type is in Herb. UC.

Monomorphic, so far as known.

France: Charente Inferieur, near La Rochelle, Billot 1914 (Bur); *ibid.*, between Yus and Fomas, *Petitmengin* in 1911 (Fl, UC); *ibid.*, Chatel Oillon, *Foucaud* in 1881 (K); Gironde, Pointe de Grave, *Foucaud* in 1881 (Bur); Gard, near Vigan, *Morthier* in 1878 (Bur); Gard, Pont du Gard, near Nîmes, *Jordan* (G, Ms); Bouches du Rhone, near Arles, *de Suffren* in 1808 (DC) type of *Barkhausia Suffreniana* DC., Prod. VII: 156 n. 23; *ibid.*, near Aix, *Reynier* in 1875 (Bur). **Italy:** Etruria, San Rossore, near Pisa, *Fiori et Béguinot* 1893 (Bur, Fl, G, BML); *ibid.*, Cascine Vecchie, *Pampanini* in 1930 (UC).

Relationship

Crepis Suffreniana is closely related to *C. apula* and less closely to *C. corymbosa*. It is much more reduced in size of floret and anther tube than either of those species. In fact its extremely small flowers and flower parts, together with the very small size of its chromosomes, make it the most reduced species in the genus. Its peculiar broadened style branches are apparently a specialized feature which goes along

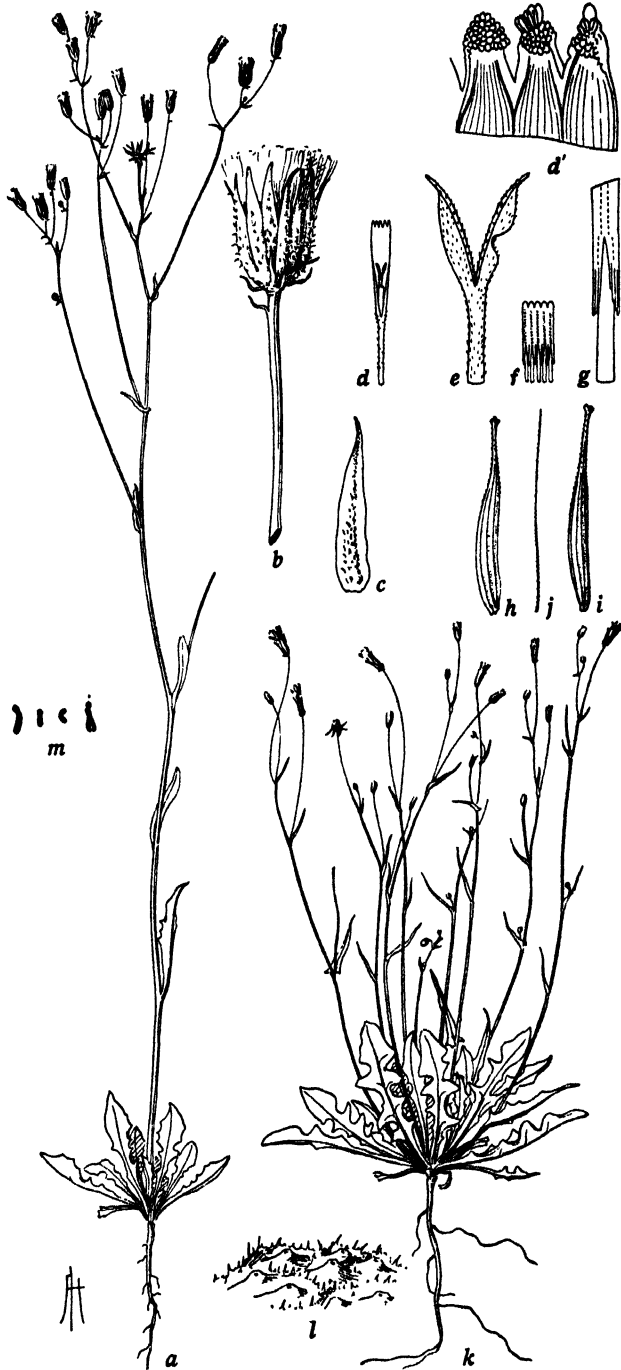


Fig. 260. *Crepis Suffreniana*, a-j, from Fiori in 1910, Fiori et Bég. Fl. It. Exs. 1393 (BML 12423); k-m, from Pampanini in 1930 (UC 429490): a, plant, $\times \frac{1}{2}$; b, fruiting head, $\times 2$; c, inner involucre bract, outer face, $\times 4$; d, floret lacking ovary, $\times 4$; d', detail of ligule teeth, $\times 50$; e, detail of style branches, $\times 32$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h-j, 2 achenes and a pappus seta, $\times 8$; k, plant, $\times \frac{1}{2}$; l, detail of receptacle, $\times 25$; m, somatic chromosomes, $n = 4$, $\times 1250$.

with the minute anther tube and limited supply of pollen, a combination of characters which has not been observed in any other species. Unfortunately, experimental hybridizations between either this species or *C. apula* and other species of this section have not been made. Cytogenetic research on such hybrids should yield evidence of significance on the evolution of the group. *C. Suffreniana* is at the apex of a phylogenetic series which seems to have had its origin in a 10-chromosome ancestor (see Part I, pp. 69, 73). Like *C. senecioides* and *C. nigricans* of sec. 27, it occurs frequently on semiarid sandy soil.

SECTION 25. LEPIDOSERIS

Of the 13 species in this section, 9 have been studied in living condition ; and they all have closely similar karyotypes except for occasional polyploid forms of *C. vesicaria*. They are mostly perennial plants, but some of the more advanced members of the group show considerable variation in length of life, which is affected by environmental conditions and season of germination. Some of these are usually monocarpic or strictly annual. In habit the plant, though well developed, may be

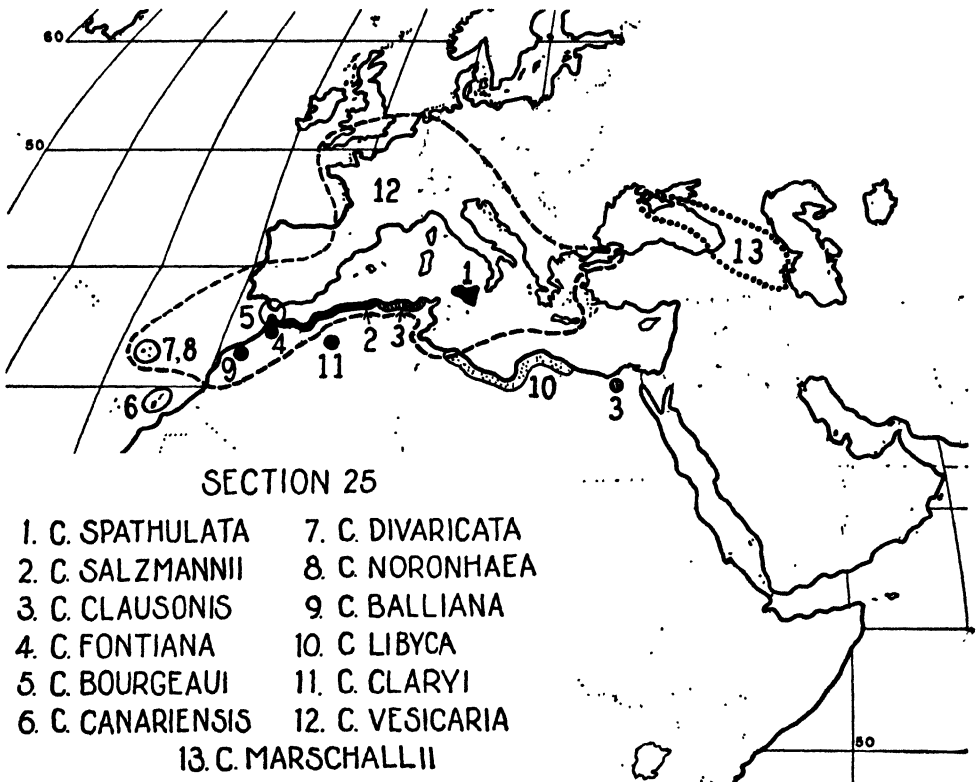


Fig. 261. Geographic distribution of the 13 species in sec. 25. The single known stations for species no. 4, no. 9, and no. 11 are shown by solid circles. Based on Goode *Base Map No. 301 HC*. By permission of the University of Chicago Press.

rather low and spreading ; or the stem may be tall and branched mostly toward the top. There is always more or less pubescence on the plants. The heads are mostly medium in size and many-flowered. The achenes are uniform in all but two of the species, and in all of them the inner (discal) achenes are always beaked and 10-ribbed.

The 13 species fall naturally into two main groups which might well have been recognized as subsections, but which will be designated here as Groups A and B. In Group A there are 3 subgroups : (1) *C. spathulata*, *C. Salzmannii*, and *C. clausonis* ; (2) *C. fontiana* and *C. bourgeaui* ; (3) *C. canariensis*, *C. divaricata*, and *C. noronhaea*. In Group B there are 5 species : *C. balliana*, *C. libyca*, *C. claryi*, *C. vesicaria*, and *C. marschallii* ; but *C. vesicaria* is a large inclusive species comprising 8 well-marked subspecies and a host of minor variants.

Group A

The 8 species in this group are all perennials and in all of them the achenes are *shortly* beaked. They are all restricted in distribution and are mostly narrow endemics. From their present distribution (cf. fig. 261) they may reasonably be considered as forerunners of the more advanced species in this section; and it is probable that they formerly had a much wider distribution and are now more or less depleted and on the way to extinction (cf. *C. divaricata*) unless rejuvenated in some way or merged with some other species (cf. *C. vesicaria* subsp. *andryaloides*).

(1) The three species in this subgroup are considered to be the most primitive ones in the section on account of their very strong woody roots, large leaves, and robust stems. *C. spathulata* and *C. Clausonis* are unique in their blooming period, which beings in late autumn and extends through the winter. One subspecies of *C. vesicaria*, namely, *hyemalis*, is also a winter-flowering plant; and, like *C. spathulata*, it is endemic in Sicily. Thus, *C. spathulata* and *C. Clausonis*, which is endemic in Tunisia and E. Algeria, occupy closely adjacent areas, whereas *C. Salzmannii* extends westward along the Algerian-Moroccan littoral.

(2) *C. Fontiana* and *C. Bourgeaui*, of the districts north and south of the Straits of Gibraltar, are considered to be next in degree of primitiveness. They show more resemblance to *C. canariensis* than to any other member of the section. It seems rather surprising that two such well-marked species should exist in their area without having been recognized long ago; and one wonders whether they are actually extremely rare and hence nearly extinct.

(3) That the three insular species, *C. canariensis* of Lanzarote and Fuerteventura Is., *C. divaricata* of Madeira, and *C. Noronhaea* of Porto Santo I. in the Madeira Archipelago, are closely related was shown by the genetic studies of Jenkins (Univ. Calif. Publ. Agr. Sci. 6: 369-400. 1939). In addition to being geographically isolated, however, they have also developed an internal isolating mechanism such that artificial hybrids between them are only fairly or poorly fertile. With their closest relatives situated on the mainland to the northeast, it is plausible to assume that they came to their present locations from that direction. The problems of migration routes, means of transportation, and possible land connections of these islands with the mainland are discussed in Part I, chapters 7 and 8.

Group B

Of the 5 species in this group, *C. Balliana* and some of the subspecies of *C. vesicaria*, including subsp. *typica*, are characterized by having biform achenes. The marginal achenes are usually beakless, more or less compressed, and paler in color than the inner ones, which are terete and long-beaked. At the same time, the strong perennial root, robust habit, and comparatively large heads and achenes of *C. Balliana* indicate that it is as primitive as most of the species in Group A. Therefore, it seems probable that *C. Balliana* was represented in the multiple ancestry of the very polymorphic *C. vesicaria*.

C. libyca is geographically isolated, except perhaps at one point near Tripoli, from *C. vesicaria*; and it is certainly isolated from *C. vesicaria tarazacifolia* to which it shows closest resemblance. It is very different, however, from the latter in numerous characters. Furthermore, artificial hybrids between *C. libyca* and *C. vesicaria typica* proved to be sterile. *C. libyca*, therefore, must be recognized as a species. Evidently it has become adapted to more xerophytic conditions than any other species in the section, except *C. Marshallii* and the following one.

C. Claryi, of the Saharan Atlas Mts., is very interesting, in that it shows some

morphological evidence of relationship with certain species in sec. 8 of tropical Africa. It, however, appears to be closest to *C. vesicaria*. Such evidence of connections with two different sections are just what may be expected in an essentially monophyletic genus, and in a region where the present-day species could easily have been influenced by the ancestors of both sections.

C. vesicaria and *C. Marschallii* are very closely related species; but the latter is more reduced in size of the heads, involucre bracts, and florets than all the subspecies of *C. vesicaria* except subsp. *myriocephala*; and the achenes of *C. Marschallii* have much longer and finer beaks than those of subsp. *myriocephala*. *C. Marschallii* appears to be completely isolated from *C. vesicaria* geographically; and, like *C. libyca*, it is especially well adapted to xerophytic conditions. The interrelationships of the various subspecies of *C. vesicaria* are discussed under that species.

Key to the Species of Section 25

A Achenes uniform, all beaked, the beak short or long; outer involucre bracts lanceolate, not imbricate, or if ovate and imbricate (*C. Fontiana*, *C. Bourgeauii*), then the plant perennial and the achenes all shortly beaked.

B Outer involucre bracts numerous, ovate, imbricate; perennial plants.

C Ligules without red on outer face; style branches green; achenes dark brown, 4–5 mm long with a beak 1 mm long; pappus white, rather persistent.....173. *C. Fontiana*, p. 807

CC Ligules with red on outer face; style branches yellow; achenes medium brown, 4.5–6 mm long, with a beak 1–2 mm long; pappus dusky-white, caducous.....174. *C. Bourgeauii*, p. 809

BB Outer involucre bracts fewer, lanceolate, not imbricate; perennial, biennial, or annual plants.

D Plants flowering in winter or early spring.

E Heads few, only 1–4 per stem. Sicily.....170. *C. spatulata*, p. 800

EE Heads more numerous.

F Caudical leaves with long petioles, denticulate or dentate; stem or stems decumbent; heads erect before anthesis; involucre finely gland-pubescent; achenes brownish-yellow, 4.5–6 mm long, with a beak about $\frac{1}{2}$ as long as the whole achene. Algeria, local.....172. *C. Clausonii*, p. 804

FF Caudical leaves with short petioles, runcinate-pinnatifid; stem erect; heads bent downward before anthesis; involucre black-setose; achenes pale brown, 5–7 mm long, with a beak nearly $\frac{1}{2}$ as long as the whole achene. Sicily.....181, b. *C. vesicaria hyemalis*, p. 833

DD Plants flowering in late spring and summer

G Achenes 4–5.5 mm long, with the beak about $\frac{1}{4}$ as long as the whole achene, or if sometimes 6–7 mm long, with the beak $\frac{1}{8}$ as long as the achene (*C. divariata* and *C. Noronhaea* of Madeira Archipelago), then the ligules deep yellow with red on outer face.

H Cauline leaves ovate, strongly amplexicaul; leaves, stem, and branches glabrous; longest outer involucre bracts $\frac{1}{2}$ – $\frac{3}{8}$ as long as the inner. Canary Is.175. *C. canariensis*, p. 812

HH Cauline leaves lanceolate or linear, not or less strongly amplexicaul; leaves, stem, and branches more or less pubescent or, if glabrous, the outer involucre bracts only $\frac{1}{2}$ as long as the inner.

I Leaves pubescent on both sides, with short pale hairs; ligules without red on outer face; achenes stramineous or pale brown. N. Morocco and Algeria, littoral.....171. *C. Salzmanni*, p. 803

II Leaves glabrous or pubescent, with black setules along veins; ligules with red on outer face; achenes dark brown or brown.

- J Caudical leaves with the petiole $\frac{1}{4}$ – $\frac{1}{2}$ as long as the blade; angles between branches and main axis narrow; involucre 10–12 mm long, 6–8 mm wide; corolla 13–19 mm long. Madeira, local. 176. *C. divaricata*, p. 814
- JJ Caudical leaves with the petiole $\frac{1}{4}$ – $\frac{1}{2}$ as long as the blade; angles between branches and main axis wide; involucre 7–10 mm long, 4–6 mm wide; corolla 10–11 mm long. Porto Santo I. 177. *C. Noronhaea*, p. 817
- GG Achenes 5–13 (mostly 6–8) mm long, with the beak $\frac{1}{3}$ – $\frac{2}{3}$ as long as the whole achene or, if the beak sometimes less than $\frac{1}{2}$ of the achene (*C. vesicaria andryaloides*), then the ligules pale yellow without red on outer face.
- K Achenes greenish or brownish-yellow, coarsely beaked and ribbed, the beak about $\frac{1}{2}$ as long as the achene, definitely ribbed; receptacle strigose, the trichomes coarse, yellow, shining.
- L Involucre dark green; style branches 3 mm long, dark green; achenes greenish-yellow. N. Morocco. 181, *g. C. vesicaria proleptica*, p. 858
- LL Involucre pale green; style branches 2 mm long, yellow; achenes brownish-yellow. E. Spain. 181, *h. C. vesicaria congenita*, p. 860
- KK Achenes dark or pale brown, finely beaked and ribbed, the beak smooth or faintly ribbed; receptacle ciliate, the cilia fine, white or, if yellowish (*C. lybica*), then the achenes with a beak $\frac{1}{2}$ – $\frac{2}{3}$ as long as the achene.
- M Involucres setose with black, often long setae; ligules pale yellow; achenes dark brown. Madeira, endemic. 181, *f. C. vesicaria andryaloides*, p. 853
- MM Involucres gland-pubescent and sometimes setulose; ligules deep yellow; achenes pale brown.
- N Achenes with a beak about $\frac{1}{2}$ as long as the achene.
- O Corolla 9–12 mm long, the ligule with red on outer face; pappus white. 181, *e. C. vesicaria taraxacifolia*, p. 843
- OO Corolla about 15 mm long, the ligule without red on outer face; pappus pale yellow. S. Algeria, local. 180. *C. Claryi*, p. 824
- NN Achenes with a beak $\frac{1}{2}$ – $\frac{2}{3}$ as long as the whole achene.
- P Involucres 11–13 mm long, 6–8 mm wide; outer involucre bracts $\frac{1}{4}$ – $\frac{1}{2}$ as long as the inner; corolla about 15 mm long, the ligule without red on outer face; achenes 9–13 mm long. Libya and N.W. Egypt. 179. *C. libyca*, p. 822
- PP Involucres 10–12 mm long, 4–5 mm wide; outer involucre bracts $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner; corolla about 10 mm long, the ligule with red on outer face; achenes 6–8 mm long. Caspian-Caucasus. 182. *C. Marschallii*, p. 863
- AA Achenes bifiform, the marginal (at least some) beakless or very shortly beaked and pale, at least on the inner face, or if sometimes uniform (*C. vesicaria typica*), then the plant usually annual or biennial and the outer involucre bracts ovate, imbricate.
- Q Heads fewer, larger, in open cymes; involucre 8–14 mm long, 3–8 (mostly 4–6) mm wide at middle; achenes 4–9 (mostly 5–7) mm long.
- R Outer involucre bracts ovate, imbricate. 181, *a. C. vesicaria typica*, p. 828
- RR Outer involucre bracts lanceolate, not imbricate.
- S Leaves dentate to pinnately parted; marginal achenes obcompressed; inner achenes with the beak usually equal to the body. 181, *d. C. vesicaria stellata*, p. 838
- SS Leaves entire or denticulate; marginal achenes laterally compressed; inner achenes with the beak shorter than the body. 178. *C. Balliana*, p. 820
- QQ Heads more numerous, smaller, in congested cymes; involucre 6–7 mm long, 2–3.5 mm wide at middle; achenes 3–4 mm long. 181, *c. C. vesicaria myriocephala*, p. 836

170. *Crepis spathulata* Guss.

Adnot. Cat. Pl. Boccad. 73. 1821; Fl. Sic. 2: 412. 1843. (Fig. 262.)

Perennial, 1.5–3 dm high; caudex 0.5–1 cm wide, tapering into a straight woody root, leafy at crown; caudical leaves 5–15 cm long, 0.5–2.5 cm wide, oblanceolate to spatulate, obtuse or somewhat acute, sinuate-dentate or -denticulate, attenuate into a short or long narrow winged petiole, glabrous or puberulent; cauline leaves small, sessile, linear, acuminate, or bractlike, puberulent; stems 2–3, erect or ascending, slender, terete, striate, simple, 1-headed, or remotely 1–2-furcate, 2–4-headed, the lower branches elongated, puberulent, canescent-tomentose at the bifurcations; peduncles 2–22 cm long, 1–3-bracteate, \pm canescent-tomentose and shortly and finely gland-pubescent at summit; heads erect, medium, many-flowered; involucre cylindric-campanulate, 12–13 mm long, 5–7 mm wide, canescent-tomentose, sparsely pubescent with short gland hairs and a few longer pale glandless hairs; outer bracts 8–10, unequal, longest $\frac{1}{3}$ as long as inner bracts, lanceolate, acute; inner bracts 12–14, in 2 series, inner ones broadly membranous-margined, lanceolate, obtuse, ciliate at tip, pubescent on inner face with appressed shining hairs, becoming carinate and spongy-thickened at base in fruit; receptacle alveolate, fimbriellae ciliate; corolla about 17 mm long; ligule 1.25 mm wide; teeth 0.25–0.5 mm long, acute; corolla tube 4 mm long, pubescent with acicular hairs 0.05–0.8 mm long; anther tube 5×1.25 mm dis., appendages 0.9 mm long, narrow, acute; filaments 0.5 mm longer; style branches 2.5 mm long, 0.1 mm wide, green; achenes brown, 5.5 mm long, 0.75 mm wide, subterete, fusiform, gradually attenuate into a beak about 1 mm long, with expanded pappus disk, constricted at the finely calloused base, 10-ribbed, ribs narrow, rounded, finely spiculate; pappus dusky white, 5 mm long, 2-seriate, fine, soft, deciduous. Flowering Oct. (Oct. to May acc. to Gussone); flowers yellow.

Barkhausia spathulata Spreng., Syst. Veg. 3: 651. 1826; DC., Prod. 7: 153. 1838.

Hieraciodes spathulatum O. Kuntze, Gen. 1: 346. 1891.

Crepis vesicaria var. *spathulata* (Guss.) Fiori, Fl. Anal. Ital. 3(2): 431. 1904.

Endemic in Sicily, where, acc. to Gussone (Fl. Sic., 2: 412. 1843), it is seen in meadows and clayey fields *from November to May*. Attempts were made by the author in 1930, and later by Professor D. Lanza of the R. Orto Botanico of Palermo, to collect specimens of this species at some of the stations listed by Gussone but without success. In the localities visited, this species seems to have disappeared, whereas *C. vesicaria* has become, or still is, a common plant. These observations may have special significance in view of the more primitive characteristics exhibited by *C. spathulata*. *C. vesicaria*, however, flowers during spring and summer, whereas *C. spathulata*, acc. to Gussone, is a winter-flowering species.

This little-known and apparently very rare or possibly extinct species has long been confused with *Crepis tingitana* (Salz.) ex Ball, owing to the citation of Salzmann's *Hieracium tingitanum* as a synonym under *Barkhausia spathulata* by de Candolle (153). That the two species were actually confused by him is shown by the fact that in the de Candolle herbarium, on the same sheet with Gussone's plant from Sicily, dated 1825, is an authentic specimen of Salzmann's species which was collected, also in 1825, near Tangier, Morocco. The two species differ, however, in many respects (cf. *C. tingitana*).

Monomorphic.

Sicily: Segeste, near Palermo, Gussone ex Herb. R. Horti Neapol. (UC) *compared with authentic specimens*; several localities in Sicily, Gussone (Naples, in herb. Guss.); 2 specimens received from Gussone in 1825 and 1831 (DC); ex herb. J. Ball, without date (K). (Cf. stations recorded by Gussone [*loc. cit.*].)

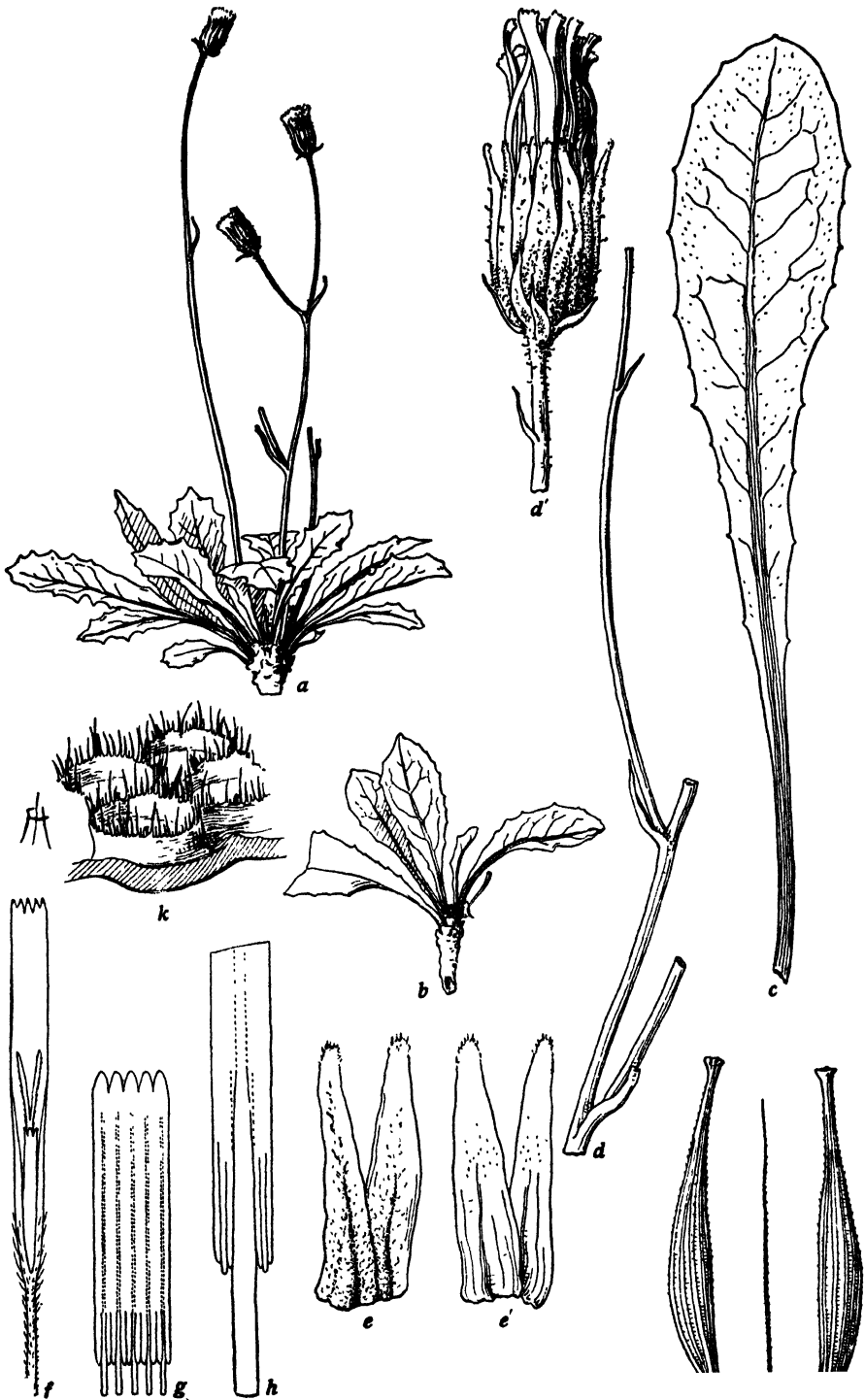


Fig. 262. *Crepis spathulata*, from authentic specimens (UC 259895): *a*, *b*, plants, $\times \frac{1}{2}$; *c*, caudical leaf, lower face, $\times 1$; *d*, part of flower stem and one pedunculate branch, $\times 1$; *d'*, head from same, $\times 2$; *e*, outer face, *e'*, inner face of 2 involucral bracts, $\times 4$; *f*, floret lacking ovary, $\times 4$; *g*, anther tube, $\times 8$; *h*, detail of appendages, $\times 32$; *k*, detail of receptacle, $\times 25$; *l-n*, 2 achenes and a pappus seta, $\times 8$.

Relationship

Crepis spathulata is closest to *C. Salzmannii* and, like it, is related, but less closely, to *C. Clausonis*. From both of these species *C. spathulata* is very distinct in the low stature, the few and larger heads, and the much larger florets. It is less close to the other more primitive species of this section.

171. *Crepis Salzmannii* sp. nov.

(Pl. 27, Fig. 263.)

Herba perennis 1.5–3.5 dm alta; radix recta lignea; caudex ligneus 1–1.5 cm latus foliatus simplex vel furcatus; folia caudicalia 8–16 cm longa 1.3–2.5 cm lata oblanceolata vel spathulata gradatim attenuata in petiolum alatum obtusa vel acuta denticulata pubescentia, pilis brevis pallidis eglandulosis; folia caulina similia vel pinnatifida superiores lanceolata acuta vel acuminata late auriculato-amplexicaulia, auriculis dentatis pubescentibus; caulis centralis erectus teretus sulcatus pubescens ab basi remote 4–5-ramosus, ramis strictis vel arcuatis oligocephalis; caules laterales arcuati vel semidecumbentes; pedunculi 1.5–5.5 cm longi stricti tomentosi interdum scabriduli; capitula erecta parva ad mediocria multiflora; involucria campanulata circa 10 mm longa 6 mm lata tomentosa interdum setulosa vel glanduloso-pubescentia, squamis exterioribus 8–10 aequalibus circa 2-plo brevioribus lanceolatis acutis, interioribus 12–16 lanceolatis obtusis ventraliter pubescentibus in dorso carinatis et spongioso-incrassatis; receptaculum areolatum breve ciliatum; corolla circa 10 mm longa, ligula 1.5 mm lata, tubo 3 mm longo pubescenti pilis brevis acicularis; antherae 3.5 mm longi; rami styli 2 mm longi virentes; achaenia straminea 4–5 mm longa subtereta in rostrum crassiusculum attenuata 10-costata ad apicem spiculata; pappus albus 4–5 mm longus 2-seriatus tenuis mollis deciduus.

Perennial, 1.5–3.5 dm high; root vertical, woody; caudex woody, 1–1.5 cm wide, simple, leafy, bearing 1 erect stem or ultimately divided with 2–3 lateral stems; caudical leaves 8–16 cm long, 1.3–2.5 cm wide, oblanceolate or spatulate, obtuse or acute, obscurely to definitely denticulate, gradually attenuate into a winged petiole with broader clasping base, pubescent on both sides with short pale glandless hairs, finely ciliate on margin; lower cauline leaves similar or \pm pinnatifid, middle and upper lanceolate to linear, acute or acuminate, broadly auriculate-amplexicaul, auricles denticulate or dentate, pubescent; central axis erect, lateral stems arcuate or semidecumbent, terete, sulcate, pubescent or puberulent, remotely 4–5-branched beginning near base, branches strict or arcuate, shortly branched at summit, bearing few-headed cymose clusters; peduncles 1.5–5.5 cm long, strict, striate, tomentulose or tomentose, sometimes scabridulous; heads erect, small to medium, many-flowered; involucre campanulate, about 10 mm long, 6 mm wide at middle, canescent-tomentose, sometimes setulose or gland-pubescent; outer bracts 8–10, nearly equal, $\frac{1}{3}$ – $\frac{1}{2}$ as long as inner bracts, lanceolate, acute, scarious-margined, sometimes setulose; inner bracts 12–16, in 2 ranks, inner broadly scarious-margined, lanceolate, obtuse, white-ciliate at tip, pubescent on inner face with appressed shining hairs, becoming carinate and spongy-thickened dorsally in fruit; receptacle areolate-fimbriate, fimbriae low, shortly ciliate; corolla about 10 mm long; ligule 1.5 mm wide; teeth 0.1–0.15 mm long; corolla tube 3 mm long, pubescent with acicular hairs 0.1–0.6 mm long, extending onto base of ligule; anther tube 3.5×1.1 mm dis.; appendages 0.75 mm long, narrow, acute; filaments 0.5 mm longer; style branches 2 mm long, 0.1 mm wide, green; achenes stramineous or pale brown, 4–5 mm long, 0.4–0.8 mm wide, subterete, broadest near base, gradually attenuate upward into a rather coarse beak 0.5–1 mm long, with expanded pappus disk, con-



Fig. 263. *Crepis Salsmannii*, from Font Quer 739 (UC 485069): a, plant, $\times \frac{1}{2}$; b, lower cauline leaf, upper face, $\times 1$; c, peduncle and head, $\times 2$; d, outer face, d', inner face of an inner involucre bract, $\times 4$; e, floret lacking ovary, $\times 4$; f, anther tube, $\times 8$; g, detail of appendages, $\times 32$; h, k, l, 2 achenes and a pappus seta, $\times 8$.

stricted at the calloused base, 10-ribbed, ribs rather strong, rounded, finely spiculate toward the apex; pappus white or dusky, 4–5 mm long, exceeding the involucre, 2-seriate, fine, soft, deciduous. Flowering Jan.–Apr.; flowers yellow.

N. W. Morocco and maritime Algeria.

The type of *C. Salzmännii* was previously identified by others as *Barkhausia taraxacifolia* and as *B. spathulata* (?), but see discussion of relationship below. The plant from Oran, identified by Battandier and Trabut (Fl. Alg., 563. 1888–1890) as *C. spathulata* Guss., may be this species. It is unfortunate that the material used for the drawings (fig. 263) was not taken from the type; but the specimen used (*Font Quer 739*, cited below) corresponds fairly well with the type, if allowance is made for the later date of collection (Apr. instead of Feb.) and for minor variations in leaf shape. A photograph of the type is in Herb. UC.

Morocco: meadows around Tangier, *Salzmann misit*, Aug., 1825 (K ex herb. J. Gay) type; Tangier and Tetuan, *Hooker* in 1871 (G); *ibid.*, *Hooker* in 1871 (K) m.v. 1, p.p.; Tandja (= Tangier), Mt. Djebel Quebir, *Font Quer 739* (UC) as *C. intybacea* Brot.; Daxar Riffien (Anyhera), fields, *Vidal and Lopez 42* (Bar). **Algeria:** maritime, *Ball* in 1856 (G).

Minor Variant of *C. Salzmännii*

1. Plant low, caudical leaves lyrate-pinnately parted, terminal segment hastate, lateral segments retrorse, and peduncles gland-pubescent. Although the plant is only 1.2 dm high, the habit, heads, flowers, and fruits are typical. The difference in the leaves, although striking, is no greater than the leaf shape variations found in many species of *Crepis*. The plant was identified by *Hooker* as a variety of *C. taraxacifolia* approaching *C. taraxacoides*. *Hooker* in 1871 (K), Tangier and Tetuan, N. Morocco.

Relationship

Crepis Salzmännii is intermediate between *C. spathulata* and *C. Clausonis*. It shows more resemblance to the latter in size and habit of the plant, size of corolla, and surface of the receptacle, whereas it resembles the former in size and shape of the achenes, pubescence of the corolla tube, and shape of the anther appendages. Yet *C. Salzmännii* is certainly distinct from its two nearest relatives in the simple but recalcitrant caudex, the auriculate-amplexicaul cauline leaves, and the congested cymose clusters of flower heads. It also differs from the two species mentioned above in its strictly spring-flowering habit. These three species are all distinct from *C. Fontiana*, *C. Bourgeaui*, and the other species of this section with shortly beaked achenes.

172. *Crepis Clausonis* (Pomel) Batt. et Trab.

Fl. Alg. 564. 1888–1890. (Fig. 264.)

Perennial, 1–3 dm high; root vertical, woody, 0.3–1 cm wide, elongated, strongly branched; caudex very short, densely pitted with old leaf scars; caudical leaves 8–15 cm long, 1.5–3 cm wide (in cult. spec. up to 32 cm long, 5 cm wide), oblanceolate, acute, gradually attenuate into a long winged petiole, denticulate or sinuately dentate, teeth corneous-mucronate, glabrous or finely pubescent with short pale glandless hairs; cauline leaves small, linear, or bractlike; stem or stems decumbent, cymosely branched and rebranched, branches several, remote, 1–3 headed, tomentulose, finely gland-pubescent or glabrescent; peduncles 1.5–12 cm long, strict or arcuate, tomentulose, often gland-pubescent, not thickened below fruiting heads; heads erect, medium, about 100-flowered; involucre campanulate, 10–12 mm long, 6–8 mm wide at middle in fruit, dark green, canescent-tomentose, finely gland-pubescent; outer bracts 6–8, nearly equal, about $\frac{1}{3}$ as long as the inner, lance-linear, acute, somewhat scarious; inner bracts 12–14, lanceolate, acute or acuminate, membranous-margined, often with a few short black setae near apex, appressed-pubescent on inner face, becoming convex and spongy-thickened at the base at full

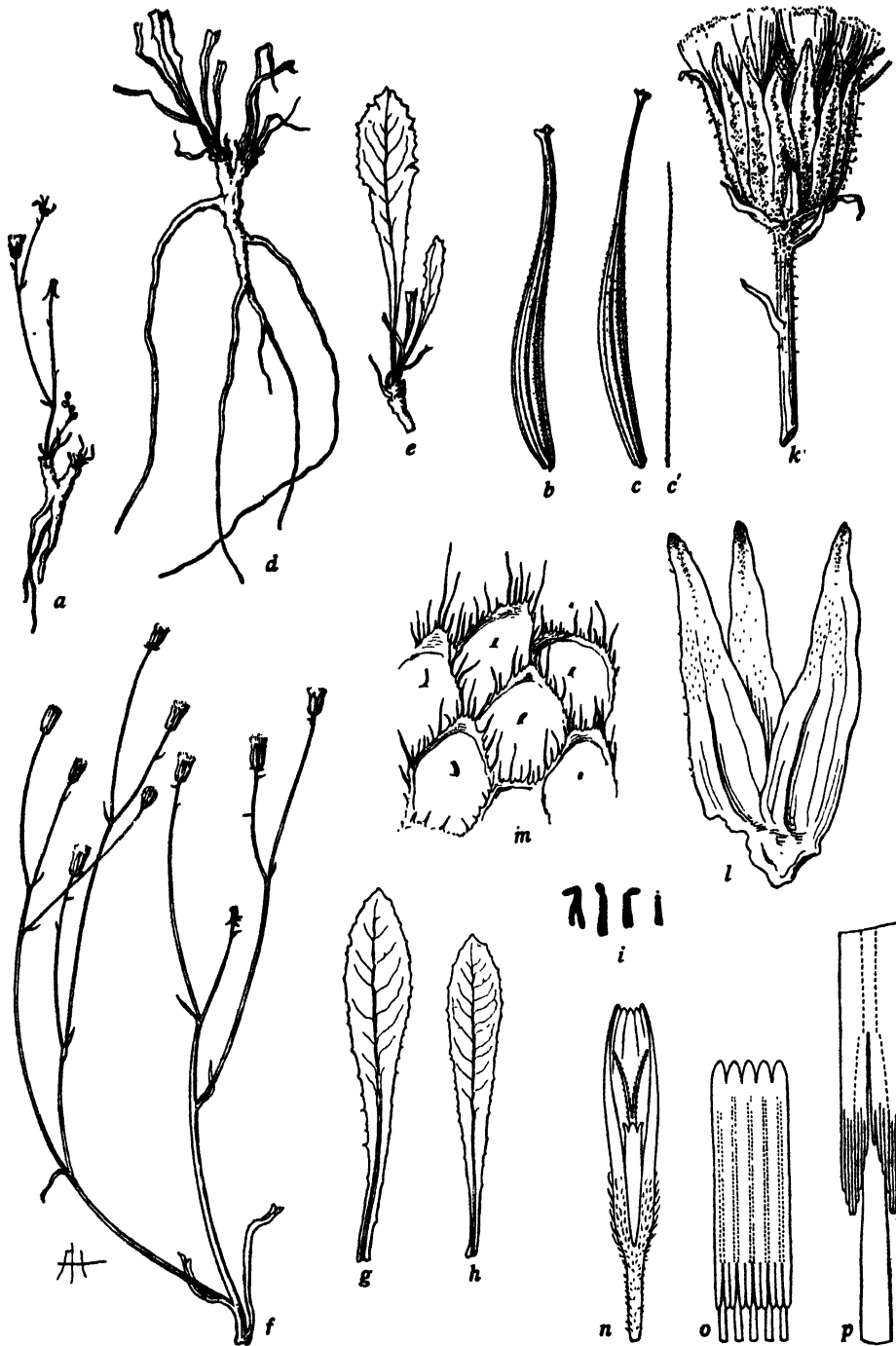


Fig. 264. *Crepis Clausonis*, a-c, from authentic specimen of Clauson (UC 429464); d, e, from Babcock #68 (UC 429438); f-p, from hort. genet. Calif. 30.2848-10 (UC 648331): a, plant taken in autumn, $\times \frac{1}{4}$; b, c, c', 2 achenes and a pappus seta, $\times 8$; d, e, plants taken June 5, $\times \frac{1}{4}$; f, flower stem with branches and heads, $\times \frac{1}{4}$; g, h, leaves, $\times \frac{1}{4}$; i, somatic chromosomes, $n = 4$, $\times 1250$; k, head, $\times 2$; l, 3 involucre bracts, inner face, $\times 4$; m, detail of receptacle, $\times 25$; n, floret lacking ovary, $\times 4$; o, anther tube, $\times 8$; p, detail of appendages, $\times 32$.

maturity, ultimately reflexed; receptacle alveolate, densely ciliate; corolla about 11 mm long; ligule 2.5 mm wide at middle, much narrower at summit and thus remaining infolded in anthesis, pubescent near base; teeth 0.1–0.3 mm long; corolla tube 3 mm long, densely pubescent with acicular hairs 0.05–0.5 mm long; anther tube 4×1.25 mm dis.; appendages 0.75 mm long, acute, united; style branches 2.25 mm long, 0.1 mm wide, yellow with green hairs; achenes brownish-yellow, 4.5–6 mm long, 0.5–0.6 mm wide, fusiform, attenuate into a definite beak 0.5–1.5 mm long, with expanded pappus disk, constricted at the finely pale-calloused hollow base, 10-ribbed, ribs narrow, rounded, finely spiculate; pappus white, 4–6 mm long, 2-seriate, about equally fine, soft, deciduous. Flowering Oct.–Nov., after the first autumn rains; flowers yellow. Chromosomes, $2n = 8$.

Barkhausia Clausonis Pomel, Nouv. Mat. Fl. Atl. 4. 1874.

E. half of Algeria, N. Tunisia, and lower Egypt. Although most of the collections reported by Battandier (Fl. Alg. 564. 1888–1890) are from stations near Algiers, yet the occurrence of the species at Constantine has been verified by the present author. Also, one of Battandier's localities is Tébessa, which is about 200 km southeast of Constantine near the Tunisian border and about 150 km from the sea. Some of the stations near Alger are very near the seashore, but others are in adjacent uplands, Tébessa being more than 1000 m above the sea and Constantine about 630 m. In Constantine the plants were growing in heavy clay soil on an exposed slope on the right-hand side of the highway running from the city to the *polygone* (an artillery depot between 1 and 2 km from the railway station). Although abundant here, the species was not seen elsewhere. At that season (June) the soil was very dry, and only short caudical leaves were found, which thus confirms in part Battandier's report that the plants produce leaves in winter and bloom after the first rains in October–November. Battandier's observation has also been confirmed by no less an authority than Dr. R. Maire of the University of Algiers, as well as by the author of the species. Under cultivation the apical part of the caudical leaves in some plants is heavily blotched with purple anthocyanin pigment.

The type is the specimen (in herb. Cosson) collected by Clauson in 1858 near Kolea, a place west of Algiers and just east of Castiglione. On the same sheet is a specimen collected by Clauson at Bers Tamail, an unknown locality. Battandier published a later note in conjunction with his proposed *C. tunetana* (q.v.) which said that numerous intermediates between *C. Clausonis* and *C. tararacifolia* exist and therefore that the former should be considered a form of the latter. In the opinion of the present author, however, none of these supposed intermediates actually has *C. Clausonis* as one parent, because it is unique among N. African *Crepis* species in its late fall or winter blooming habit. Presumably these "intermediates" of Battandier should all be included under *C. vesicaria*. It is unfortunate that no definite locality was given by Letourneux for his collection in lower Egypt (see spec. cited below), since no other collections of this species from Egypt are known to me. Although I have no notes on the flowers and fruits, Letourneux's plant, judging from the decumbent habit and the thick perennial root, appears to be this species.

Monomorphic.

Algeria: Berbessu, near Coleah (Kolea), *Clauson* in 1858 (PC) type; Bers Tamail, *Clauson* (PC); Mitidja, plain of Mazafran, *Clauson* (UC ex Herb. Alger) authentic; La Reghaia, *Battandier* in 1886 (Rome); *ibid.*, *Battandier* in 1889 (Ms); Rouiba, near Alger, *Battandier et Trabut* in 1885 (BB, UCf); Constantine Prov., *Du Kerley* (B); Constantine city, clayey banks between the city and the *polygone*, *Reboud* 1709 (K, PC, UWG) as *Barkhausia macrophylla* Spr.; Constantine city, Belle Vue, *Garrigues* in Oct., 1906 (UC ex herb. Maire) with flowers and fruits; Constantine city, 1–2 km from railway station, right side of road to the *polygone*, *Babcock* 268

(UC); ex hort. genet. Calif. 30. 2848-5, 10, cult. from roots of *Babcock 268* (UC). Tunisia: Ain Draham, *Rubert 377* (PC). Lower Egypt: *Letourneux* in 1870 ? (PC).

Relationship

Crepis Clausonis is certainly one of the more primitive species of this section. Its thick, deeply penetrating root may make it an even stronger perennial than *C. spathulata* or *C. Salzmanni*. Apparently these other two have not been able to maintain themselves in nature to the extent that *C. Clausonis* has. Also, in size of leaves and flower heads, *C. Clausonis* is just as primitive as they are. But in *C. Clausonis* the corolla and anther tube are shorter than in *C. spathulata*; and the achenes are narrower and have longer, more slender beaks than those in *C. Salzmanni*. For these rather arbitrary reasons, *C. Clausonis* is placed third in the series.

173. *Crepis Fontiana* Babc., ex Maire

Bull. Soc. d'Hist. Nat. Afr. Nord 29: 427. 1938. (Fig. 265.)

Perennial, 1-1.5 dm high, gland-pubescent throughout, or lower leaves glabrous; root straight, elongated, slender, woody; caudex 6-10 mm wide, marked with leaf scars below, leafy above; caudical leaves up to 19 cm long, 3 cm wide, oblanceolate, acute, runcinately dentate or pinnatifid and finely denticulate, lateral segments triangular, acute, gradually attenuate into a broadly winged petiole; lower cauline leaves ovate or oblong, acute or acuminate, irregularly dentate or retrorsely pinnatifid, broadly amplexicaul, auricles rounded, denticulate, middle and upper cauline leaves similar or entire, gradually reduced, uppermost bractlike; stem divaricately 2-4-branched near base, axis short, cymosely 4-5-headed, branches decumbent, remotely 1-2-branched near base or simple, cymosely 3-4-headed; peduncles 1-6 cm long, rather stout, not thickened near head in fruit; heads erect, medium, about 100-flowered; involucre cylindric-campanulate, 10-12 mm long, 6-8 mm wide in fruit; outer bracts 8-12, imbricate, $\frac{1}{3}$ as long as inner bracts, ovate, apiculate, rounded and white-ciliate at very tip, glabrous or sparsely pubescent, green or purplish in mid-region, broadly membranous-margined, becoming lax; inner bracts 10-16, lanceolate, obtuse and white-ciliate at tip, dark green, narrowly membranous-margined, densely gland-pubescent with very short dark setules and fine pale hairs, glands white, ventrally pubescent with fine white hairs, becoming carinate and infolded, partly enclosing marginal achenes, the keel thickened and indurate, not spongy-thickened, ultimately strongly reflexed; receptacle convex, areolate-fimbriate, fimbriae low, membranous, densely ciliate with fine white hairs 0.25 mm long; corolla 10 mm long, ligule 1.75 mm wide; ligule teeth 0.15-0.25 mm long, triangular; corolla tube 2.75 mm long, pubescent with acicular hairs 0.05-0.75 mm long; anther tube 3.5 \times 1.2 mm dis.; appendages 0.6 mm long, oblong, obtuse; filaments 0.5 mm longer; style branches 1.75 mm long, 0.15 mm wide, acuminate, green; achenes dark brown, 4-5 mm long, curved or straight, subterete, 0.5-0.7 mm wide, abruptly attenuate to the very narrow finely calloused base, more gradually attenuate into a slender beak about 1 mm long, with expanded pappus disk, 10-ribbed, ribs narrow, rather prominent, rounded, very finely muriculate under lens; pappus white, 4-5 mm long, 2-3-seriate, fine, soft, semipersistent. Flowering Mar.; flowers deep yellow¹ without red on ligules. Chromosomes, $2n = 8$.

N.W. Morocco.

Monomorphic.

¹ In our 1934 culture of this species grown from protected seed from two plants, half of the plants had pale lemon yellow florets, pale green style branches, and deep yellow anther tubes and pollen grains. As such flowers had not been seen in this species during the 3 years it had been under cultivation, it was inferred that this new type was the result of a mutation.

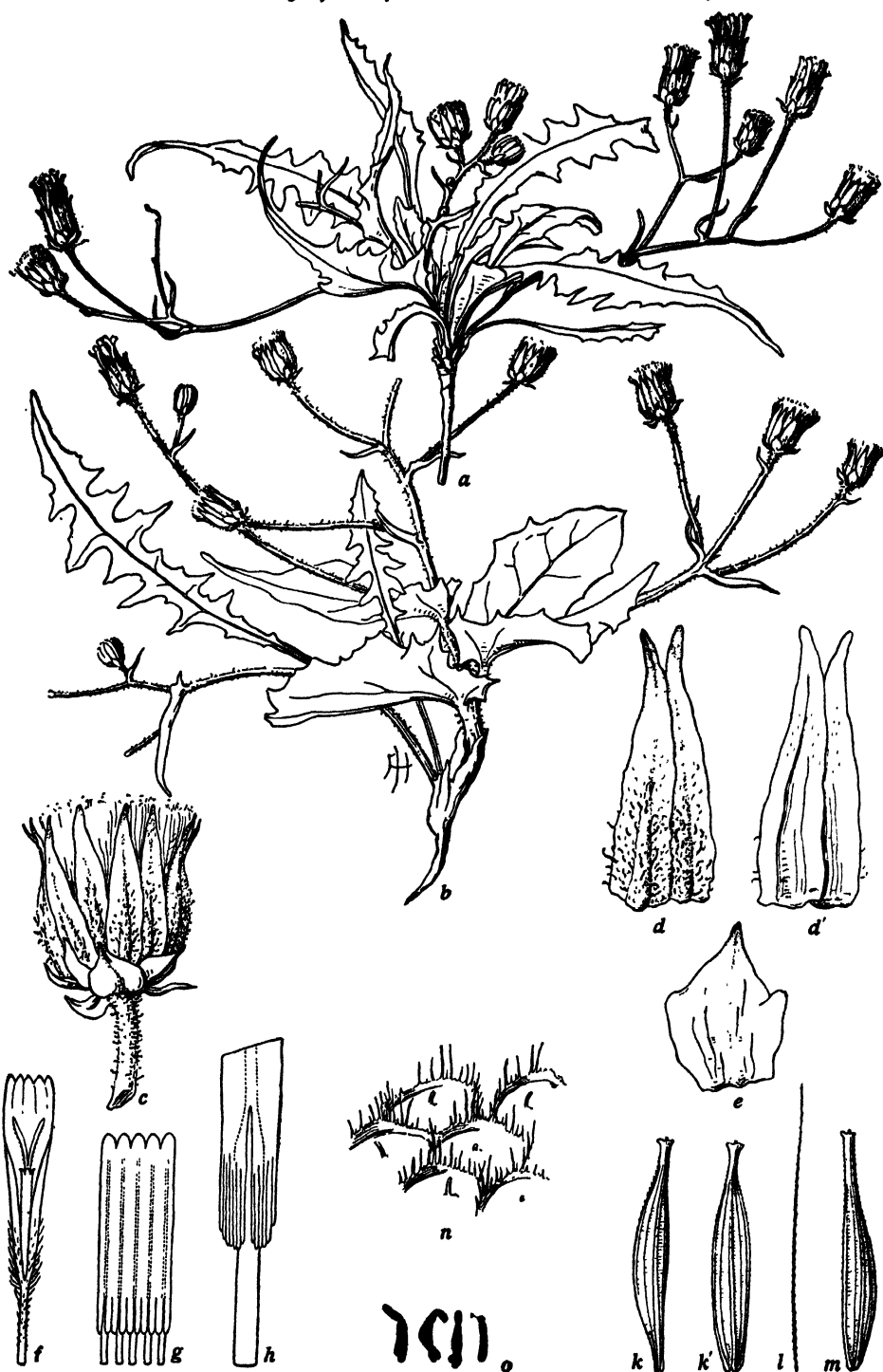


Fig. 265. *Crepis Fontiana*, from type (UC 485070; hort. genet. Calif. 3225): *a, b*, plants, $\times \frac{1}{2}$; *c*, mature head, $\times 2$; *d, d'*, 2 inner involucre bracts united at base, outer and inner face, $\times 4$; *e*, outer involucre bract, $\times 4$; *f*, floret lacking ovary, $\times 4$; *g*, anther tube, $\times 8$; *h*, detail of appendages, $\times 32$; *i-m*, marginal achene (two views), pappus seta, and inner achene, $\times 8$; *n*, detail of receptacle, $\times 25$; *o*, somatic chromosomes, $n = 4$, $\times 1250$.

Morocco: near El Araix (Larache), among herbs, *Font Quer* 740 (UC 485070) type. Named for Dr. P. Font Quer, who collected the type in 1930 and determined the specimen as *Crepis erythra* Pau, which is said by Pau to be intermediate between *C. tarazacifolia* and *C. vesicaria* (but see discussion of relationship below).

The fragmentary specimen, *Gandoger* in 1910–1911 (Mo), collected at “Kas Faraoum,” Morocco, is probably this species. It, however, lacks the glandular pubescence of the type; the stems are glabrous; the leaves pubescent with short stout pale glandless hairs; the inner involucre bracts tomentose but neither pubescent nor hairy dorsally. There are no fruits and no mature florets. “Kas Faraoum” is probably a misspelling of Kas Faraoun, the Arabic name commonly used for the ruins of the ancient Roman city, Volubilis, near Meknes, between Rabat and Fez, which assumption, if true, would indicate that *C. Fontiana* occurs in the interior of W. Morocco at least to a distance of about 100 km from the coast.

Relationship

Crepis Fontiana is nearest to *C. Bourgeaui* from which it is easily distinguished by the low divaricate habit, the less dissected caudical leaves, the broadly amplexicaul cauline leaves, the indurate but not spongy-thickened inner involucre bracts, the green style branches, shorter achenes, and shorter, more persistent pappus. It is rather close to *C. canariensis*, and the Madeiran species, *C. divaricata* and *C. Noronhaea*, all of which are even more distinct from it and more advanced in degree of specialization of the involucre. On this basis, *C. Fontiana* is the least advanced species in this group. The chromosomes of *C. Fontiana* are closely similar to those of its nearest relatives. Experimental crosses between *C. Fontiana* and both *C. divaricata* and *C. Noronhaea* produced highly fertile hybrids, but these two insular species are widely separated from *C. Fontiana* geographically. *C. Fontiana* was also crossed experimentally with *C. vesicaria tarazacifolia*, which indicates that, if these two species should meet, they would cross naturally, provided that they were not isolated by some physiological factor such as time of flowering. But these experimental crosses produced hybrids with only 50 per cent or less fertility. Furthermore, *C. vesicaria tarazacifolia* either does not occur in N.W. Morocco or is comparatively rare. Only 2 collections of it from W. Morocco are known to the writer, and these came from farther south, near Casa Blanca. But, even if *C. tarazacifolia* or some other subspecies of *C. vesicaria* does exist with *C. Fontiana*, it seems likely that any hybrids which might occur naturally would be sufficiently sterile to minimize the danger of swamping out *C. Fontiana*. For the present, therefore, the recognition of *C. Fontiana* as a species appears to be justified.

174. *Crepis Bourgeaui* Bab.

Ex Maire, Bull. Soc. d'Hist. Nat. Afr. Nord 29: 428. 1938. (Pl. 28. Fig. 266.)

Perennial, 2–5 dm high; root straight, elongated, woody, 4–8 mm wide near caudex; caudex swollen, 5–12 mm wide, leaf-scarred below, leafy above; caudical leaves up to 21 cm long, 7 cm wide, oblanceolate, acute, pinnately parted with close or remote unequal oblanceolate acute dentate segments, gradually attenuate into a broad or narrow winged petiole with broader base, pubescent with short pale glandless hairs or glabrescent; lower cauline leaves similar or sessile, middle and upper ones linear, acuminate, entire, denticulate or laciniate, narrowly amplexicaul, gradually reduced, uppermost bractlike; stem erect, rather stout, few-leaved, 1–3-branched from very near base, branches elongated, equal to axis, like axis corymbosely few-branched near summit, flowering branches pedunculate or 2–3-headed, stem and lower branches fistulose, purplish below, sulcate, glabrous, ob-

scurely hispidulous or tomentulose; peduncles 1–11 cm long, strong, arcuate, sulcate, slightly thickened near head in fruit, canescent-tomentulose, very finely and shortly gland-pubescent, glands small, brown; heads erect, medium, many-flowered; involucre cylindric-campanulate, 10–12 mm long, 5–7 mm wide in fruiting heads; outer bracts 8–14, nearly equal, $\frac{1}{3}$ – $\frac{1}{2}$ as long as inner bracts, imbricate, ovate-lanceolate, acute or acuminate, glabrous or sparsely tomentulose, brownish-green medianly, broadly membranous laterally, becoming scarious, lax; inner bracts 10–18, lanceolate, obtuse, white-ciliate, ventrally appressed-pubescent, dorsally canescent-tomentose, shortly and finely gland-pubescent below, glabrescent near tip, becoming strongly carinate medianly, spongy-thickened near base, ultimately reflexed; receptacle areolate, densely ciliate between areoles, cilia white, 0.5 mm long; corolla 10 mm long; ligule 1.25 mm wide, pubescent near base with several-celled acicular hairs up to 0.75 mm long; teeth 0.1–0.2 mm long; corolla tube 4 mm long, densely beset near base with stout papilliform hairs up to 0.75 mm long and near base of ligule with short acicular hairs; anther tube 3.25×1 mm dis.; appendages 0.5 mm long, oblong, acute; filaments very short, only 0.4 mm longer; style branches 1.75 mm long, 0.1 mm wide, attenuate, yellow; achenes medium brown, 4.5–6 mm long, 0.5–0.7 mm wide, somewhat curved, subterete, constricted near the narrow hollow-calloused base, attenuate into a beak 1–2 mm long, pale and funnel-form below pappus disk, 10-ribbed, ribs narrow, rounded, muriculate; pappus dusky white, 5–6.5 mm long, 2–3-seriate, fine, soft, caducous. Flowering Mar.–May; flowers yellow, reddish on outer face of ligules and ligule teeth. Chromosomes, $2n = 8$.

S. Spain, in Andalusia, near Cadiz, and N. Morocco, around Tangier. The type locality is Puerto de Santa Maria, Cadiz, Spain, where it was collected by E. Bourgeau, for whom it is named. One of the specimens from Tangier was collected by Salzmann at an earlier date, but until more material is available there is some uncertainty whether the Moroccan plants cited below are as typical of the species as are Bourgeau's specimens. It is unfortunate that a more definite locality was not recorded for the two specimens of Gros cited below, but from the low altitude it is very probable that the station is somewhere in the Andalusian littoral.

Spain: Cadiz, Puerto de Santa Maria, sandy seashore, *Bourgeau* in 1849 (P type, UCf, K); *ibid.*, *Rojas* in 1940 (UC 639622); Andalusia, between Rute and Puerto de Santa Maria, 30 m, *Gros* in 1925 (Bar, UC) m.v. 1, 2. **Morocco:** around Tangier, vineyards, *Salzmann misit 1825* (K) m.v. 3; Tangier and Tetuan, *Hooker* in 1871 (K) m.v. 3.

Minor Variants of *C. Bourgeaui*

1. Very robust, heads in anthesis larger than type, fruiting heads lacking. Plant 5+ dm high; root lacking; stem and cauline leaves typical; involucre in anthesis 12 mm high, 7 mm wide; outer bracts 8–10; inner bracts 10–14; corolla 14 mm long; ligule 1.75 mm wide, pubescent near base; corolla tube 5 mm long, barbellulate and shortly pubescent; anther tube 4.25×1.25 mm dis.; appendages 0.7–0.8 mm long, oblong, acute; filaments 0.4–0.6 mm longer; style branches 2.5 mm long, 0.15 mm wide, attenuate, yellow; achenes (immature) and pappus typical. Flowering May; flowers yellow, reddish on outer face of ligules and teeth. The large size of plant, heads, and flowers suggests the possibility that this is a polyploid form, but examination of pollen showed no 4-pored grains present, although the grains are irregular in size (24–34, average 30μ). (Pl. 28, b.) *Gros* in 1925 (Bar), among herbs, 30 m, between Rute and Puerto de Santa Maria, Andalusia, Spain.

2. Stem, peduncles, and involucre canescent-tomentulose, not gland-hairy; corolla 13–14 mm long; anther tube 4 mm long; style branches 2 mm long. Plant 20 cm high; root straight, 4 mm wide; caudex 1 cm wide; caudical leaves up to 15 cm long, 4 cm wide, remotely pinnately parted; cauline leaves similar or sessile, amplexicaul, linear, acuminate; stem erect, 2-branched from near base, branches equal to axis, 4-branched above, branches pedunculate; involucre in fruit 12 mm long, 6–7 mm wide; outer bracts 10–12; inner bracts 12–16; achenes (not fully mature) 5–6 mm long, beak 1.5 mm long; pappus 5 mm long, dusky white. The large florets might indicate that this

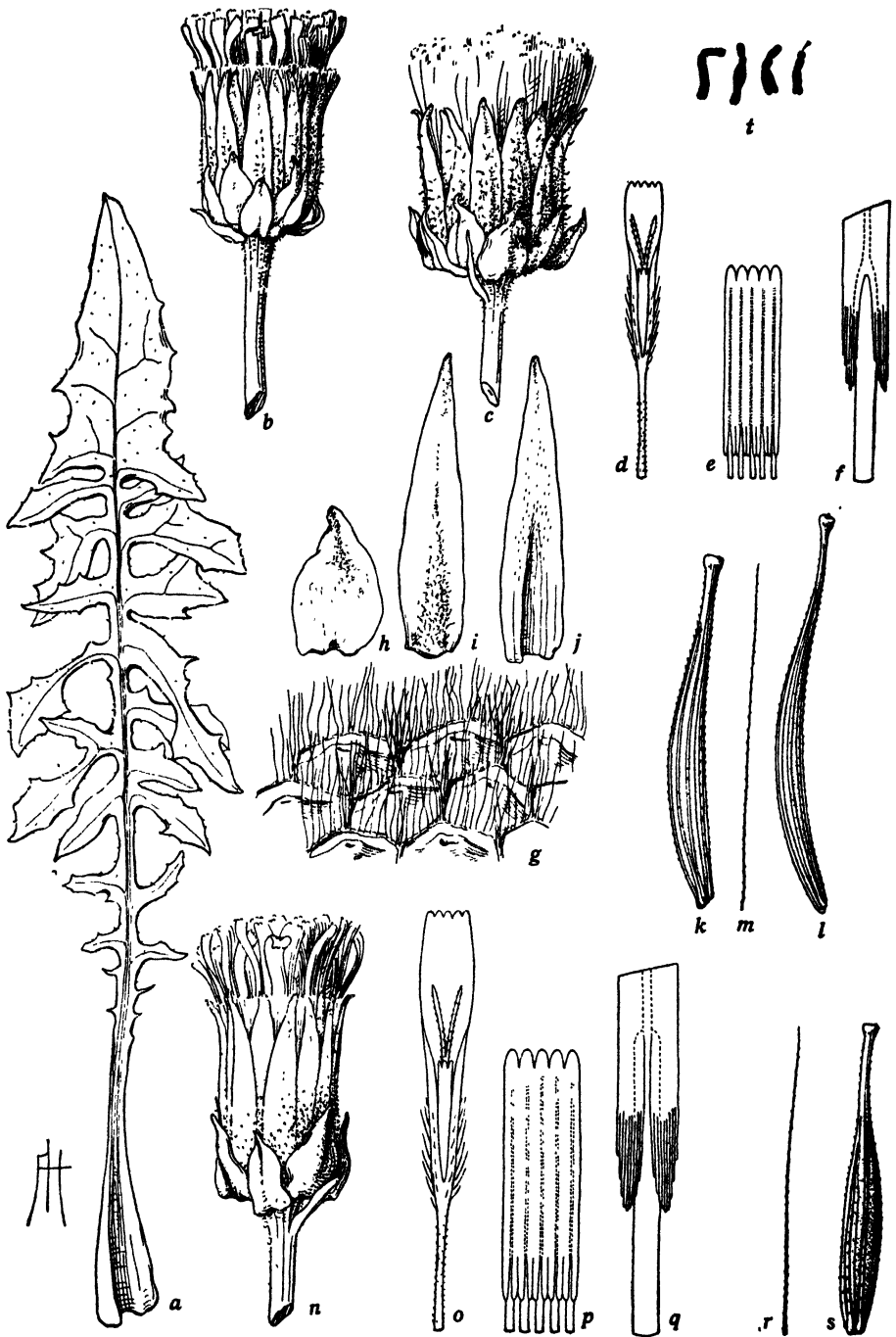


Fig. 266. *Crepis Bourgeaui*, a-m, from type (P) and isotype (K); n-s, from Gros in 1925 (Bar, UC 519495); t, from hort. genet. Calif. 3475 (grown from seeds collected at type locality by J. Rojas through Sr. Ramon Sala, Barcelona): a, caudal leaf, $\times 1$; b, immature head, $\times 2$; c, mature head, $\times 2$; d, floret lacking ovary, $\times 4$; e, detail of ligule teeth, $\times 50$; f, anther tube, $\times 8$; g, detail of receptacle, $\times 32$; h-j, outer and 2 inner involucre bracts, $\times 4$; k-m, 2 achenes and a pappus seta, $\times 8$; n, flowering head, $\times 2$; o, floret lacking ovary, $\times 4$; p, anther tube, $\times 8$; q, detail of appendages, $\times 32$; r, s, achene and pappus seta, $\times 8$; t, somatic chromosomes, $n = 4$, $\times 1250$.

is also a polyploid of some sort, but here, also, no 4-pored grains were seen, and the size of the grains was the same as in m.v. 1. Even though apparently collected at the same station as m.v. 1, the stature of m.v. 2 is very much lower than m.v. 1, a feature worthy of note. These two plants of Gros, however, may represent the more usual forms of the species. It must be admitted that the type collection probably grew on sterile soil. Additional material and especially field studies are needed. (Pl. 28, c.) *Gros* in 1925 (UC), among herbs, 30 m, between Rute and Puerto de Santa Maria, Andalusia, Spain.

3. Size and habit of plant more like that in *C. vesicaria*, with which species it was previously confused; heads slightly smaller than in type and in m.v. 1 and 2. Plant 3–3.7 dm high; root straight, 4 mm wide; caudex 5–8 mm wide; caudical leaves up to 16 cm long, 4.5 cm wide; pinnately or bipinnately parted with linear segments; cauline leaves similar or sessile, amplexicaul, middle ones \pm lacinate; stem erect, remotely branched from near base or about middle upward, branches long and, like axis, corymbosely 3–4-pedunculate near summit; involucre in fruit 9–10 mm high, 5–7 mm wide; outer bracts 9–12, broadly lanceolate to narrowly ovate; inner bracts 12–18, typical; corolla 10–11 mm long; ligules reddish on outer face; style branches brown in sic.; achenes 4.25–5 mm long, typical; pappus dusky white, 5 mm long, caducous. Flowering April; flowers yellow. Although Hooker determined his two plants as *C. taraxacifolia*, he noted the shorter achenes. But these differ from *C. vesicaria taraxacifolia* not only in size; they are exactly like those of the type of *C. Bourgeau*, except slightly smaller. Field studies are needed in both Morocco and Spain in order to determine the range of variation within the species, especially in size and habit of plant, and in order to ascertain the more frequent forms, as well as the genetic nature of extreme variants. (Pl. 28, d.) *Salzmann misit 1825* (K ex herb. J. Gay), vineyards around Tangier; *Hooker* in 1871 (K), Tangier and Tetuan, N. Morocco.

Relationship

C. Bourgeau is closest to *C. Fontiana*, from which it is readily distinguished by the erect taller plant, pinnately or bipinnately parted caudical leaves, narrowly amplexicaul lower cauline leaves, ligules and ligule teeth reddish-purple on outer face, style branches yellow, achenes longer and longer beaked, pappus longer and caducous. Like *C. Fontiana*, it is also close to *C. canariensis*, but less close to *C. divaricata* and *C. Noronhaea*.

175. *Crepis canariensis* (Sch. Bip.) Babec.

Univ. Calif. Publ. Agr. Sci. 6(13): 369. 1939. (Fig. 267.)

Perennial, 1.5–3.5 dm high; caudex thick, fleshy, cylindric or fusiform; caudical leaves rosulate, numerous, up to 18 cm long, 6 cm wide, obovate-lanceolate or elliptic, obtuse or acute, attenuate into a winged petiole $\frac{1}{3}$ as long as blade with broader clasping base, irregularly dentate and denticulate, glabrous on both sides; lower cauline leaves similar, middle and upper ones triangular-cordate, acute or acuminate, strongly dilated at base, denticulate, glabrous; stem robust, divaricately branched from or near base, terete, sulcate-striate, glabrous; branches arcuately ascending, equal to or longer than the central axis, the lower branches sometimes much branched, ultimate branches 1–4-headed, corymbiform; peduncles canescent-tomentulose or glabrescent and sometimes very finely gland-pubescent; heads medium, always erect, nearly hemispherical before anthesis, broadly urceolate at maturity, many-flowered (105 florets in a head, acc. to Schultz); involucre broadly campanulate, up to 8 mm broad at base and 11 mm high, dark green, canescent-tomentose at base, pubescent with short fine glandless hairs which are yellowish or black near tips of bracts; outer bracts 10, linear, acute, unequal, longest $\frac{1}{2}$ – $\frac{2}{3}$ as long as inner ones; inner bracts 13–18, nearly equal, lanceolate, rather strongly attenuate toward the obtuse finely ciliate tip, ventrally pubescent with short shining hairs, becoming broadly carinate, partly enclosing marginal achenes, pale spongy-thickened at the base, remaining erect at maturity; receptacle alveolate-fimbrillate, alveolae 0.5 mm wide, separated by thin narrow fimbrillae thickly beset with fine yellowish hyaline trichomes 0.1 mm long; corolla 10–13 mm long; ligule 2–3 mm



Fig. 267. *Crepis canariensis*, a-f, from Bourgeau 1242 (K); g-i, from type (K); j, from a specimen in herb. Lowe (K); k, from hort. genet. Calif. 3049 (grown from seeds collected on Lanzarote I. by Dr. O. Burchard; cf. UC 463896, 463897): a, plant, $\times \frac{1}{2}$; b, head, $\times 2$; c, inner involucre bract, inner face, $\times 4$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g-i, 2 achenes and a pappus seta, $\times 8$; j, detail of receptacle, $\times 25$; k, somatic chromosomes, $n = 4$, $\times 1250$.

wide; teeth 0.2 mm long, dark green or purplish on outer face; corolla tube 4 mm long, pubescent, hairs very short near base, longer and acicular at summit; anther tube (3)4 \times 1.2 mm dis.; appendages 0.7 mm long, obtuse; filaments 0.7 mm longer; style branches 1.5–2 mm long, slender, yellow; achenes light brown, 4–4.5 mm long, 0.6–0.7 mm wide at middle, subterete, fusiform, attenuate into a beak 0.75–1 mm

long, 0.15 mm wide, with slightly expanded pale pappus disk, abruptly narrowed at the oblique calloused base, 10-ribbed, ribs narrow, finely spiculate, especially toward summit; pappus 4 mm long, sordid white, fine, soft, caducous. Flowering March–July; flowers deep yellow. Chromosomes, $2n = 8$.

Crepis Loweii var. *canariensis* Sch. Bip., ex Webb et Berth., Phyt. Canar. 3: 461. 1836–1850.

Barkhausia hieracioides Lowe, ex Webb et Berth., loc. cit.—det. apud Lowe in litt., sed cfr. Lowe, Fl. Mad. 1: 559. 1868.

Canary Is. Type locality Lanzarote I., summit of Mt. Peñitas de Chache. Most collections are from Fuerteventura I.; but Lowe (loc. cit.) states that he found this species not uncommonly from January to April on all the heights about Aria in the north of Lanzarote in 1858–1859. Furthermore, Burchard (Biblioth. Bot. 98: 220. 1929) states: "It is so abundant on the shores of both Lanzarote and Fuerteventura, as well as in the interior of the islands, that I can detect particular stations from a distance." Acc. to Burchard (loc. cit.), this plant is well known to the natives by its purple dye, which is called *serraje de la vieja*.

Monomorphic.

Lanzarote: summit of Mt. Peñitas de Chache, Webb, "dedit 1835" (K, UCf) type or isotype; Los Valles, among rocks, Pitard 243 (Mo); without locality, Heer in 1856 (Fl); ex hort. genet. Calif. 32.3049–8, cult. from seed collected in Lanzarote by Dr. O. Burchard in 1931 (UC). **Fuerteventura:** on rocks, Tuinese (= Barranco de Tuinese according to Schultz). Bourgeau 1242 (K, MW, UCf); Valdebron, Bourgeau in 1846 (PC ex herb. Sch. Bip.); without locality, Heer in 1856 (Fl, UCf); Oliva, rocks and borders of cornfields, in 1859 (K ex herb. Lowe); Mt. Atalaya, in 1859 (K ex herb. Lowe); Mt. Atalaya, in 1859 (G ex herb. Lowe) m.v. 1. **Canary Is.:** Mt. Gaudier, Bourgeau in 1852 (B).

Minor Variant of *C. canariensis*

1. Achenes only 3 mm long, 0.5 mm wide, beak 0.5–0.75 mm long. Lowe in 1859 (G), Mt. Atalaya, Fuerteventura.

Relationship

Crepis canariensis is closely related to *C. divaricata* and *C. Noronhaea*, but is very distinct from both and is somewhat more primitive in involucre and floral characters. In this respect it stands next to *C. Bourgeaui* and *C. Fontiana* (q.v.).

176. *Crepis divaricata* (Lowe) F. Schultz

Flora 23: 719. 1840. (Fig. 268.)

Perennial, or biennial, 2–4.5 dm high; root long, woody; caudex 0.5–1 cm long, and as broad, covered with black bases of old leaves; caudical leaves numerous, up to 21 cm long, 6 cm wide, lanceolate to elliptic or oblanceolate, acute or obtuse, entire, denticulate, dentate or upper part of blade pinnately cleft with broad acute often retrorse lobes, the terminal lobe hastate, attenuate into a winged petiole $\frac{1}{4}$ – $\frac{1}{3}$ as long as blade with broader clasping base, glabrous or rarely with black erect setules on both sides along veins; cauline leaves lanceolate to linear, acuminate or acute, sessile, cordate-amplexicaul, shortly auriculate, glabrous, uppermost bractlike; stem erect, robust, up to 1 cm wide at base, sulcate, glabrous, often purplish, branched from base upward, lower branches often longer than axis, leaving axis at angle of 20–30°, \pm arcuate, paniculately branched, secondary branches corymbosely 1–5-headed, upper stem, branches, and peduncles gland-setulose with short black setules and brown glands; peduncles 1–5 (7) cm long, stout, arcuate, sparsely tomentulose near head; heads erect, large, before anthesis 9 \times 6 mm, early heads in anthesis 3–4 cm wide, with up to 100 florets; involucre cylindric-campanulate, becoming turbinate at maturity, 10–12 mm long, 6–8 mm wide at base, canescent-tomentulose, shortly gland-pubescent with pale capillary hairs, sometimes, also, with



Fig. 268. *Crepis divaricata*, a-m, from Babcock 203 (UC 429544, 513243); n, o, from Lowe 699 (DC): a, plant from type locality, $\times \frac{1}{4}$; b, flower head, $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule teeth, $\times 50$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, plant from hort. genet. Calif. 32.2980-28, $\times \frac{1}{2}$; g, fruiting head, $\times 2$; h, detail of receptacle, $\times 25$; i, somatic chromosomes, 32.2980, $n = 4$, $\times 1250$; k-m, caudical leaves, $\times \frac{1}{2}$; n, o, achene and a pappus seta, $\times 8$.

black setiform hairs; outer bracts 7–9(12), appressed, $\frac{1}{3}$ as long as inner bracts, lanceolate, ciliate at tip, margin definitely purple; inner bracts 12–15, lanceolate, acute, ciliate at tip, becoming strongly carinate, conspicuously spongy-thickened at base, pubescent on inner face; receptacle alveolate, ciliate, alveolae 0.5 mm wide, fimbriae low, cilia up to 0.3 mm long; corolla 13–19 mm long; ligule 2–2.9 mm wide; teeth 0.2–0.4 mm long; corolla tube 3 mm long, pubescent with acicular hairs; anther tube (3.75)5.5 \times 1.1(1.25) mm dis.; appendages 0.7 mm long, oblong; filaments 0.6 mm longer; style branches 2.75–3 mm long, 0.1 mm wide, attenuate, yellow; achenes uniform or marginal ones curved, dark brown, 5–7 mm long, 0.6–0.7 mm wide, fusiform, subterete, narrowed at the darkly calloused base, attenuate into a rather coarse beak 1–2.5 mm long, with expanded pappus disk, 10-ribbed, ribs broad, rounded, finely spiculate; pappus 3.5–4.5 mm long, sordid white, 2-seriate, rather fine, soft, somewhat persistent. Flowering April–July; flowers chrome yellow without red on ligules. Chromosomes, $2n = 8$.

Borkhausia divaricata Lowe, Trans. Camb. Phil. Soc. 4: 26. 1833.

Barkhausia divaricata Lowe, ex DC., Prod. 7: 157. 1838.

Hieraciodes divaricatum O. Kuntze, Gen. 1: 346. 1891.

Madeira Is. Known in its typical form only from the type locality, Promontory of San Lorenzo on "Ilheo dos Embarcadores" = Ilha de Cevada, the easternmost point of the island. It is not surprising that forms from the Desertas (small islands southeast of Madeira) exhibit some morphological differences. Their existence may be significant as indicating that this was once a widespread species. But it is just as probable that this and the other Madeiran species of *Crepis* were brought from the mainland by birds or strong winds (see Part I, pp. 135–136).

On this promontory of San Lorenzo, which is the only station on Madeira where this plant has been known to exist for the past century, the plants grow in gravelly loam on a basaltic formation near the sea among grass and other low herbs. This area having been used as pasture for a herd of goats, the species had been nearly exterminated at the type locality when the author visited it in 1930. The succulent foliage of this species makes it a valuable forage plant, it even being reported by Lowe that, in the months of April and May in the middle years of the nineteenth century, residents of Machico brought plants of this species to the mainland in boatloads to feed to their pigs.

Madeira: Pta. San Lourenço, Lowe 699, May 17, 1832 (DC, K, Ucf) type collection; *ibid.*, maritime meadows, Mandon 152 (K, Bo, Ucf, P); *ibid.*, Ilheo dos Embarcadores, Lowe in 1855 (K); *ibid.*, W. slope of the more western of the two hills among rocks, Babcock 203 and ex hort. genet. Calif. 32.2980 (UC). **Desertas:** "Flat Dez'a" (= Deserta Grande †), Lowe 862, June 3, 1850 (K, G) m.v. 1; Desertas, near Madeira, Lippold, July, 1837 (K) m.v. 2.

Minor Variants of C. divaricata

1. Uppermost cauline leaves and involucre densely pubescent with short and long brown gland hairs, the long hairs sometimes up to 3 mm long, sometimes glandless; achenes brown, not quite as dark as in typical *C. divaricata* but darker than those of *C. Noronhaea*, 5.5–6 mm long, 0.6 mm wide, like typical *C. divaricata* in shape, beak, and ribs; pappus 3.5 mm long, sordid white, rather persistent. Lowe 862, June 3, 1850 (K, G), Flat Dez'a = Deserta Grande †, Madeira Is.

2. More slender; heads narrower, peduncles and involucre densely gland-pubescent; achenes about 5 mm long; pappus about 3 mm long. Lippold, July, 1837 (K), Desertas, near Madeira.

Relationship

C. divaricata is close to *C. Noronhaea*, but observations on living plants have shown the two to be distinct species (see synoptical comparison of characters under *C. Noronhaea*). *C. divaricata* is also close to *C. canariensis* and *C. Fontiana* and is, like them, a rather primitive member of this section. Under cultivation it hybridizes

naturally with other species, such as *C. vesicaria taraxacifolia*, producing in some instances progeny which resemble certain forms of *C. vesicaria andryaloides*. Even though its artificial hybrids with *C. Noronhaea* are highly fertile, the complete geographic isolation of these two species insures them against contamination.

177. *Crepis Noronhaea* Babc.

Univ. Calif. Publ. Agr. Sci. 6(13): 369. 1939. (Fig. 269.)

Perennial or biennial, 0.8–1.8 dm high; root woody, straight, tapering; caudex up to 8 mm long, 6 mm wide, leafy, often 2–3-branched; caudical leaves lanceolate or oblanceolate, acute, acuminate or sometimes obtuse, denticulate, dentate or pinnately cleft or parted, terminal segment narrow, entire, lateral segments remote, narrow, lanceolate, attenuate into a narrow petiole $\frac{1}{3}$ – $\frac{1}{2}$ as long as blade or equal to blade and with broader clasping base, glabrous or with black erect setules; cauline leaves narrow, lanceolate or oblanceolate, shortly petioled or sessile, subamplexicaul, slightly or not auriculate, uppermost bractlike, glabrous; stem erect, slender, terete, striate, tomentose or glabrous, divaricately branched from base upward, lower branches usually longer than axis, spreading or decumbent, leaving stem at an angle of 80–90°, paniculately branched, secondary branches 1–4-headed; peduncles slender, 1–7 cm long, canescent-tomentose, sometimes sparsely gland-pubescent; heads erect, rather small, up to 80-flowered; involucre cylindric, sometimes becoming turbinate, 7–10 mm long, 4–6 mm wide at middle; outer bracts 6–9, about $\frac{1}{3}$ as long as inner bracts, lanceolate, acute, tomentose, sometimes wholly purple; inner bracts 10–13, lanceolate, acute or obtuse, white-ciliate at tip, becoming rounded carinate and spongy-thickened at base, tomentose, sometimes sparsely gland-pubescent or -setulose, pubescent on inner face, ultimately reflexed; receptacle alveolate-fimbriate, alveolae 0.4–0.6 mm wide, fimbriae low, with white cilia 0.3 mm high; corolla up to 11 mm long; ligule 1.5 mm wide, pubescent near base; ligule teeth 0.2–0.3 mm long, truncate or acute; corolla tube 3 mm long, pubescent with acicular hairs 0.05–0.5 mm long; anther tube (3.75)4 × 1.1(1.25) mm dis.; appendages 0.5 mm long, oblong, acute or obtuse; filaments 0.4–0.5 mm longer; style branches 1.75–2.5 mm long, 0.1 mm wide, deep yellow; achenes all similar or marginal ones curved, brown, 4.5–6 mm long, subterete, narrowed above the small pale-calloused base, gradually attenuate into a rather coarse beak 0.5–1.5 mm long, with expanded pappus disk, 10-ribbed, ribs prominent, extending to summit, finely spiculate; pappus white, 3–4 mm long, 1–2-seriate, fine, soft, rather persistent. Flowering Feb.–May; flowers chrome yellow with red on outer face of ligule. Chromosomes, $2n = 8$.

Borkhausia divaricata var. *pumila* Lowe, Trans. Camb. Phil. Soc. 4: 26. 1833.

Barkhausia divaricata var. *pumila* Lowe, ex DC., Prod. 7: 157. 1838.

The publication of *Crepis pumila* Rydb., Mem. N. Y. Bot. Gard. 1: 462. 1900, makes it impossible to retain this specific epithet. Named for Sr. A. C. de Noronha, Director, Museu Regional, Funchal, Madeira, who sent the seed from which experimental cultures were grown.

Porto Santo Island, Madeira Archipelago. Known only from the type locality. Certain small specimens of *C. divaricata* from the Desertas were mistaken by Lowe for *C. Noronhaea*, which accounts for his inclusion of the Desertas in the geographic distribution of this species.

Porto Santo I.: cornfields above the town, Lowe 67, May, 1828 (P, UCf) type; common in fields and waste places of the island, ex herb. Webb (Fl, UCf); Heer in 1853 (Bo, UCf); Cockerell in Jan., 1921 (US); ex hort. genet. Calif. 3022, cultivated from seed collected in Porto Santo and sent by Sr. Noronha in 1930 (UC); back of the beach, up the Rib. do Cochim, a hollow lane, Lowe, Apr. 19, 1855 (K, UCf) m.v. 1.

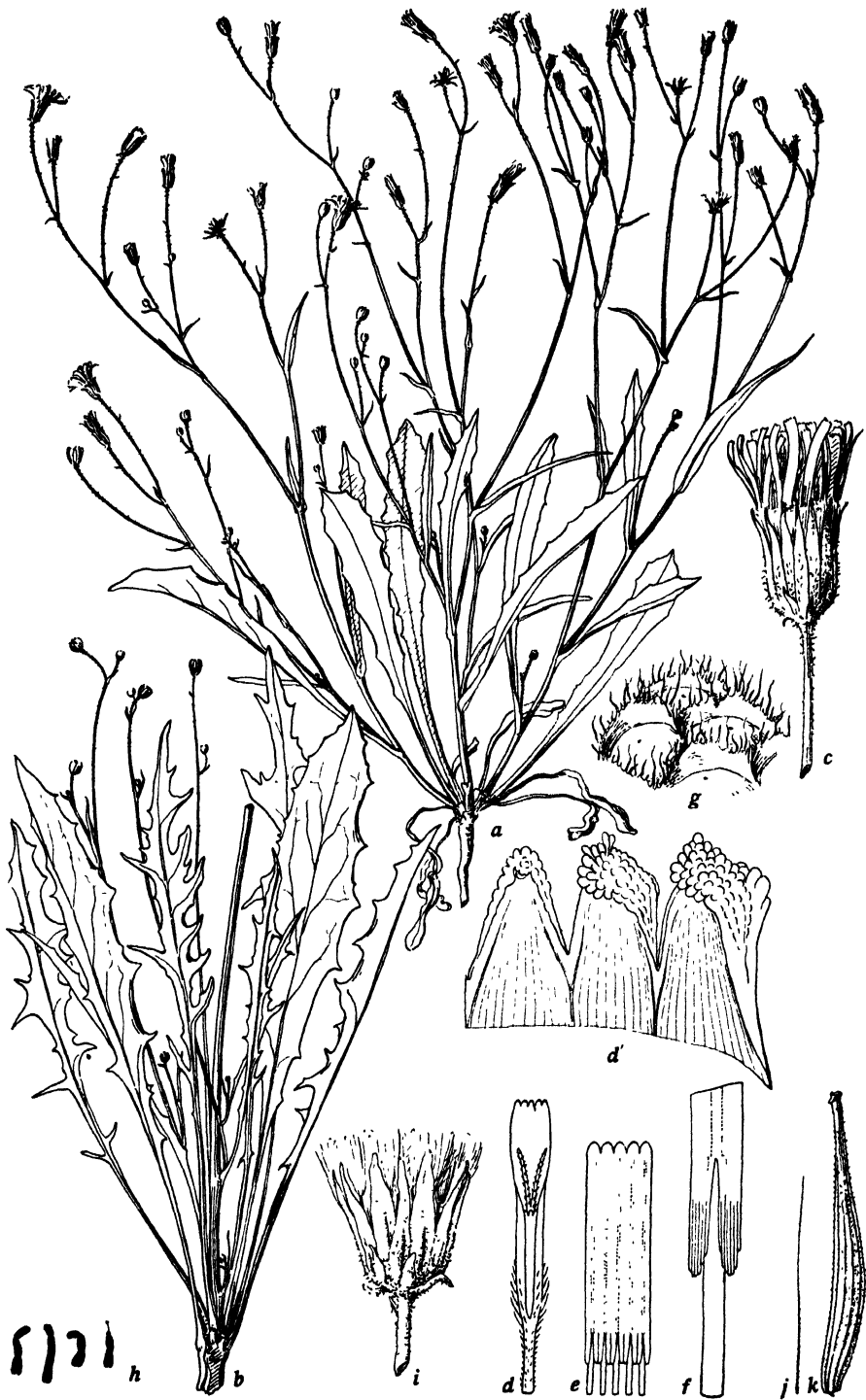


Fig. 269. *Crepis Noronhaea*, a-h, from hort. genet. Calif. 3022 (UC 506840, 513295); i-k, from type (P): a, plant showing usual habit, $\times \frac{1}{2}$; b, lower part of plant, $\times \frac{1}{2}$; c, flower head, $\times 2$; d, floret lacking ovary, $\times 4$; d', detail of ligule teeth, $\times 50$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, detail of receptacle, $\times 25$; h, somatic chromosomes, $n = 4$, $\times 1250$; i, fruiting head, $\times 2$; j, k, achene and a pappus seta, $\times 8$.

TABLE 19
SYNOPTICAL COMPARISON OF THE CHARACTERS DISTINGUISHING *CREPIS DIVARICATA*
FROM *C. NORONHAEA*

(Based largely upon data from cultivated specimens)

<i>C. divaricata</i>	<i>C. Noronhaea</i>
Caudical leaves	
<p>very numerous up to 26 cm long, 6 cm wide lanceolate to elliptic dentate to entire or upper half pinnatifid with close broad triangular lateral lobes and broad hastate terminal lobe petiole broad, alate, $\frac{1}{4}$–$\frac{1}{3}$ as long as blade</p> <p>color elm green texture waxy anthocyanin, when present on surface, localized in black spots 2–3 cm wide or in larger brown spots near indentations</p>	<p>fewer up to 20 cm long, 4.5 cm wide lanceolate or oblanceolate entire, denticulate, dentate or pinnatifid throughout with remote narrow lanceolate lateral lobes and narrow terminal lobe petiole narrow, $\frac{1}{8}$–$\frac{1}{2}$ as long as blade or equal to blade color cress green texture less waxy anthocyanin rarely present, if present the spots much larger and irregular</p>
Lower cauline leaves	
<p>broadly lanceolate sessile, amplexicaul rounded or acutely auriculate</p>	<p>narrowly lanceolate or oblanceolate shortly petioled or sessile, subamplexicaul slightly or not auriculate</p>
Stem and branches	
<p>appearing about 120 days after sowing robust 36–44(70) cm high glabrous at base regularly branched from base upward branches slightly longer than axis stem-branch angle 20–30°</p>	<p>appearing 130–200+ days after sowing slender 22–36(50) cm high tomentose at base usually divaricately branched from near base branches longer or shorter than axis stem-branch angle 80–90° for lower branches; upper ones about 30°</p>
Inflorescence	
<p>heads usually more numerous and congested branchlets 2–5-headed peduncles stout, pubescent with many purplish gland hairs, sparsely tomentose heads before anthesis \pm conical, sparsely tomentose, gland-pubescent</p> <p>first flowers open 130–170 days after sowing first heads in anthesis 3–4 cm wide florets up to 100 per head corolla up to 19 mm long style branches about 3 mm long</p>	<p>heads usually less numerous, less congested branchlets 1–2 (sometimes 3–4)-headed peduncles slender, less or not at all gland- pubescent, usually densely tomentose heads before anthesis cylindric, truncate, densely tomentose, sparsely gland-pubes- cent</p> <p>first flowers open 140–200+ days after sowing first heads in anthesis about 2.5 cm wide florets up to 80 per head corolla up to 14 mm long style branches about 2 mm long</p>

TABLE 19—(Continued)

<i>C. divaricata</i>	<i>C. Noronhaea</i>
Mature heads	
involucre turbinate, shedding florets early, up to 7 mm wide at base	involucre sometimes turbinate, sometimes cylindric, shedding florets later, up to 6 mm wide at base
outer bracts 7-9, up to 4 mm long, closely appressed, glabrous, purple on margin	outer bracts 6-9, up to 3 mm long, somewhat lax, tomentose, entirely purple, somewhat purple, or green
inner bracts up to 15, up to 12 mm long	inner bracts up to 13, up to 10 mm long
Achenes and pappus	
achenes dark brown 5-7 mm long beak 1.5-2.5 mm long pappus 3.5-4.5 mm long, sordid white	achenes usually paler brown 4.5-6 mm long beak 0.5-1.5 mm long pappus 3-4 mm long, white

Minor Variant of C. Noronhaea

1. More robust; caudical leaves numerous, runcinate-pinnate from apex to base of blade, but lateral segments broad. Probably an ecad or a variant caused by a transient chromosome deviation, since no plants resembling it appeared among the progeny reared from seed collected at Porto Santo. The more robust aspect and peculiar lower leaves probably caused Lowe to label this specimen var. A (= *C. divaricata*), although he also gave it the number, 67, which was his number for the original collection of this species in 1828. This earliest collection, however, he actually labeled *B. divaricata* nob., only giving it the varietal name, *pumila*, in his original description published in 1833. Lowe in 1855 (K), back of the beach, up the Rib. do Cochim ("or Cochino, near the town to the westward," Lowe, Fl. Mad. 1: 554. 1868), Porto Santo.

Relationship

Crepis Noronhaea is close to *C. divaricata* and was merged with it by Lowe, who was misled by the reduced nature of the *C. Noronhaea* plants which he collected in Porto Santo in 1828 and by the occurrence of reduced forms of *C. divaricata* in the Desertas, a group of small islands about 48 km southeast of Madeira. Through the kind help of Sr. A. C. de Noronha, Director of the Regional Museum in Funchal, it has been possible to compare living plants of both species. From the study of this material the following outline, showing the differences in the two species, has been prepared. From this comparison it is clear that *C. Noronhaea* is smaller than *C. divaricata* in all its parts. The species differ also, as shown in table 19, in numerous morphological and physiological characters. Yet they are obviously closely related. Thus, it may logically be inferred that *C. Noronhaea* originated from *C. divaricata*, presumably, since the chromosomes of the two species are closely similar, through gene mutations which accompanied or followed isolation.

178. *Crepis Balliana* sp. nov.

(Pl. 29. Fig. 270.)

Herba perennis circa 3 dm alta; folia caudicalia circa 10 cm longa 2.5 cm lata oblanceolata acuta denticulata in petiolum alatum attenuata; folia caulina infera circa 7 cm longa lanceolata acuminata integra acute auriculata amplexicaulia altera gradatim reducta summa bracteiformia; caules 2 vel 3 robusti arcuati sulcati remote ramosi, ramis inferis elatis ad summitatem cymose ramosis cum 3-6 capitulis; pe-

dunculi 1–6 cm longi, arcuati; capitula erecta mediocria multiflora; involucria cylindrico-campanulata in fructu circa 8 mm longa 3 mm lata, squamis exterioribus circa 7 lanceolatis quam interioribus circa 3-plo brevioribus, interioribus circa 14 lanceolatis in fructu carinatis ultimo reflexis; achenia biformia, exterioribus stramineis glabris circa 5 mm longis 0.75 mm latis columnaribus ad apicem gradatim attenuatis in ventrali planis 3-angularibus in dorso convexis et costatis, interioribus fuscis circa 7 mm longis 0.5–0.6 mm latis subteretis in rostrum brevioribus et tenuiorem gradatim attenuatis 10-costatis costis crassiusculis spiculatis; pappus albus circa 5 mm longus involucrum excedens.

Perennial (?), about 3 dm high; caudex 7 mm wide; caudical leaves about 10 cm long, 2.5 cm wide, oblanceolate, acute, sinuately denticulate, attenuate into a broadly winged petiole; lower cauline leaves about 7 cm long, lanceolate, acuminate, entire, acutely auriculate, amplexicaul, the others gradually reduced, uppermost bractlike; stem 2 or 3, robust, arcuate, sulcate, remotely branched from near base, lower branches elongated, cymosely few-branched above, 3–6-headed; peduncles 1–6 cm long, arcuate, somewhat thickened near the head; heads erect, medium, many-flowered; involucria cylindric-campanulate, about 8 mm long, 3 mm wide in fruiting heads; outer bracts about 7, lanceolate, about $\frac{1}{3}$ as long as the inner; inner bracts about 14, lanceolate, becoming carinate in fruit, ultimately reflexed; achenes biform; marginal achenes stramineous, smooth, 5–5.5 mm long, 0.75 mm wide, columnar, gradually attenuate to the apex, with narrow pappus disk, ventrally flat with a median and lateral angles, dorsally convex and few-ribbed, with an oblique basal scar; inner achenes pale brown, 6.5–7.5 mm long, 0.5–0.6 mm wide, subterete, gradually attenuate into a rather fine beak less than $\frac{1}{2}$ as long as the body, with expanded pappus disk, 10-ribbed, the ribs rather strong, close, rounded, spiculate; pappus white, about 5 mm long, exceeding the involucre.

Known only from the type specimen which was seen by me in Herb. Kew in 1925. Unfortunately, when I inquired about this specimen in 1927, it could not be found; but it may still be in existence. I had, however, obtained a photograph of the plant, the negative of which, taken by Mr. G. Atkinson, was left at Kew. This photograph has been reproduced in pl. 29. Also, a print and a few achenes, taken from the type, are on file in the Herbarium of the University of California.

Monomorphic.

Morocco: Casablanca, *Hooker* in 1871 (K, UC) as *C. tingitana* det. J. Ball.

Relationship

C. Balliana was at first mistaken by me for a variant, possibly a tetraploid, of *C. amplexifolia*. But it is apparently a perennial plant, and the achenes actually show greater similarity to those of *C. vesicaria* subsp. *typica* and *myriocephala* than to those of *C. amplexifolia*. Furthermore, the inner achenes are definitely like those of other species in this section rather than any species of sec. 26 (cf. fig. 270). They strongly resemble those of *C. vesicaria proleptica* except that the beak is finer and the ribs are not so broad. The marginal achenes, as well as the leaves and habit of the plant, might well be those of an ancestor of *C. vesicaria myriocephala*, which

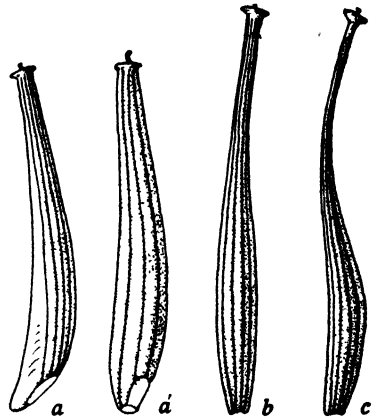


Fig. 270. *Crepis Balliana*, from type (K): a, a', marginal achene; b, c, 2 inner achenes; all, $\times 8$.

has a perennial or biennial root. The fact that this species has been collected only once in a region which has been visited by a number of collectors over a period of 70 years may indicate that it is extremely rare or has become extinct. A thorough search for it in the region of the type locality should be made. Determination of its phylogenetic position in the section is complicated by the phyletic range represented within *C. vesicaria*. Its place between *C. Noronhaea* and *C. libyca* is based on its assumed perennial habit and the comparatively short beak of the inner achenes.

179. *Crepis libyca* (Pamp.) Babç.

Univ. Calif. Publ. Bot. 19: 401. 1941. (Fig. 271.)

Perennial or biennial, 1–3 dm high; root strong, woody, tapering from the swollen caudex; caudex 1–2 cm wide, simple, leafy; caudical leaves 7–20 cm long, 2–6 cm wide, oblanceolate, acute, coarsely dentate to runcinate-pinnatifid or pinnately parted with triangular acute denticulate or dentate segments, gradually reduced into the short broadly winged petiole with broader clasping base, segments and teeth corneous-mucronate, ciliate at margin, glabrous or puberulent on both sides; lower cauline leaves similar or sessile, middle and upper ones lanceolate, acuminate, dentate or pinnatifid with narrow acuminate lobes or lacinate near base, uppermost reduced or bractlike; stem erect, robust, sulcate, puberulent, several-branched from below the middle or at the base, lower branches elongated, strict or arcuate, the branches bearing 1–7 heads in close clusters at summit, aggregate inflorescence a corymbiform compound cyme, upper stem, branches, and peduncles \pm tomentulose and/or densely gland-pubescent with short fine pale or dark hairs; peduncles 1–6 cm long, rather stout, arcuate; heads erect, large, many-flowered; involucre cylindric-campanulate, 11–13 mm long, 6–8 mm wide at middle, \pm canescent-tomentulose and gland-pubescent; outer bracts 8–16, nearly equal, $\frac{1}{4}$ – $\frac{1}{3}$ as long as inner bracts, 1.5–3 mm wide, ovate to lanceolate, acute, with broad or narrow scarious margins, sometimes with a few very short black setules near tip; inner bracts 13–18, in 2 series, innermost with broader scarious margins, lanceolate, acute, pubescent on inner face, becoming dorsally carinate and spongy-thickened in fruit, ultimately reflexed; receptacle alveolate, fimbriate low, densely ciliate, cilia 0.25 mm long; corolla 15 mm long; ligule 1.75 mm wide, pubescent at base with acicular hairs up to 0.5 mm long; teeth 0.2–0.6 mm long, gland-crested, with an anterior lip bearing large gland cells and a few stalked acicular hairs; corolla tube 5.5 mm long, pubescent from base to summit with stout acicular hairs 0.1 mm long; anther tube 3.75×1 mm dis.; appendages 0.7 mm long, oblong, acute; filaments 0.75 mm longer; style branches 1.75 mm long, 0.15 mm wide, yellow; achenes pale brown, 9–13 mm long, the body 0.5 mm wide, fusiform, attenuate into a very fine beak 1–2 times as long, with expanded pappus disk and a very narrow pale basal callosity, 10-ribbed, ribs narrow, rounded, muriculate; pappus white, 5 mm long, 2–3-seriate, very fine, soft, persistent, exceeding the involucre. Flowering Mar.–Apr.; flowers yellow. Chromosomes, $2n = 8$.

Crepis taraxacifolia var. *libyca* Pamp., Nuovo Gior. Bot. Ital. n.s., 24: 158. 1917.

Maritime Libya and N.W. Egypt.

Monomorphic.

Libya: Cirenaica, Bengasi, near Lake Bedafam, *Zanon 528* (Fl) type; *ibid.*, Raaba, Cafis, Giok Kebir, *Zanon 562c, 574, 606* (Fl, UCf); Bengasi, *Ruhmer 225* (B, UCf); *ibid.*, Petrovich in 1882 (B); Derna, *Vaccari* in 1912 (Fl); Wady Derna, *Taubert 332* (B); Marmarique, Mirsa Badia, *Schweinfurth 80* (Bo, UCf); Burgasino, *Cavara* in 1922 (UC); Tripolitania, Tripoli, *ex herb. Bentham* (K). **Egypt:** El Sellum, Wady El Ramla, *Shabetai* in 1934 (UC).

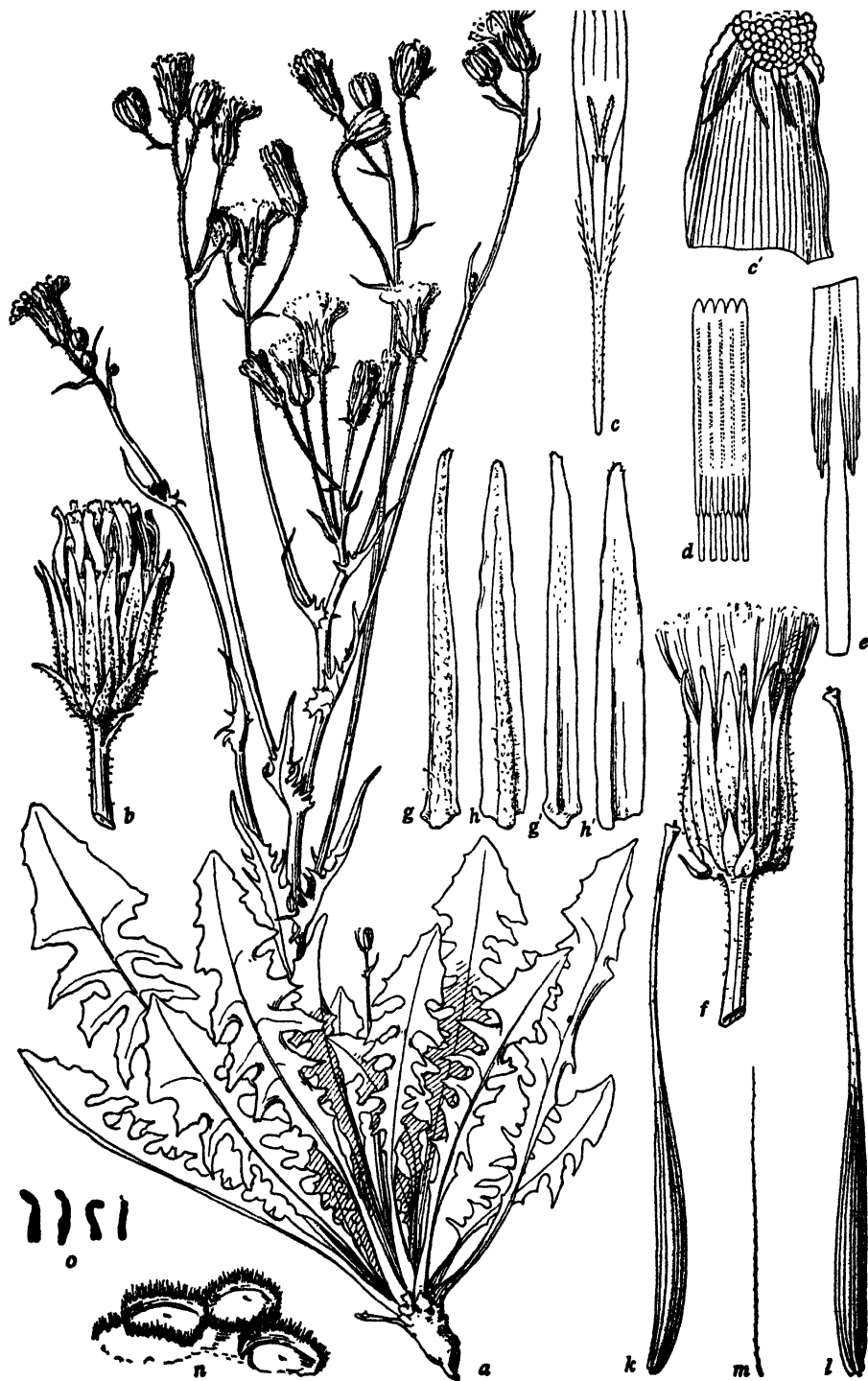


Fig. 271. *Crepis libyca*, a, from Ruhmer 225 (B); b-e, from Zanon in 1916 (Fl); f-m, from Cavarra in 1922 (UC 277221); n, o, from hort. genet. Calif. 27.1698-14 (UC 506830): a, plant, \times ca. $\frac{1}{2}$; b, flowering head, \times 2; c, floret lacking ovary, \times 4; c', detail of ligule teeth, \times 50; d, anther tube, \times 8; e, detail of appendages, \times 32; f, fruiting head, \times 2; g, h, inner involucre bracts, outer face, \times 4; g', h', *ibid.*, inner face, \times 4; k-m, marginal and inner achenes and a pappus seta, \times 8; n, detail of receptacle, \times 25; o, somatic chromosomes, $n = 4$, \times 1250.

Relationship

Crepis libyca is closely related to *C. vesicaria*, especially to subsp. *taraxacifolia*, in that the achenes are uniform in shape. It is distinct from *C. vesicaria* in the much larger heads, florets, and achenes and in the peculiar labiate ligule teeth and the yellow style branches; also the outer involueral bracts vary in shape from lanceolate to ovate and in the width of the scarious margins. This species appears to be intermediate between *C. vesicaria typica* and the more primitive *C. vesicaria proleptica*, although it is more like the former in its finely beaked achenes. It has not been crossed with *C. vesicaria typica*, but with subsp. *taraxacifolia* it produced sterile hybrids, whereas with subsp. *myriocephala* it produced more or less fertile hybrids. Thus, there is some genetic evidence to support its status as a species, and it appears to be completely isolated from all the subspecies of *C. vesicaria*.

180. *Crepis Claryi* Batt.

Ex Batt. et Trab., Fl. Alg. (Dicot.) 563. 1888–1890. (Fig. 272.)

Biennial, monocarpic (?), 4–5 dm high, hispid with white glandless hairs; root vertical, 7 mm wide at the base of the somewhat swollen leafy caudex; leaves thick, glaucous; caudical leaves 3–10 cm long, 0.5–2 cm wide, oblanceolate, acute, irregularly runcinate-pinnatifid with acute teeth or segments, gradually attenuate into a winged petiole; cauline leaves few, the lowest nearly as large as the caudical leaves, oblanceolate, broader at base, the others gradually reduced, lanceolate or linear, acutely dentate or denticulate, subamplexicaul; stem erect, remotely 4–5-branched from above or below the middle, branches strict, branched near the summit, the branchlets pedunculate, forming 4-headed corymbiform cymes; peduncles at maturity 2–9 cm long, rather stout, slightly thickened near the head; heads erect, medium, at least 60-flowered; involucre campanulate, 10–12 mm long, about 5 mm wide at middle in fruit, canescent-tomentose, setulose with a mediodorsal row of pale glandless setules on both outer and inner bracts, gland-pubescent with short brown hairs near the base; outer bracts 6, about $\frac{1}{3}$ as long as the inner, linear, somewhat scarious; inner bracts 10, in 2 ranks, the inner broadly membranous-margined, lanceolate, obtuse at the ciliate apex, strongly nerved on lower half and densely appressed-pubescent on upper half of inner face, becoming carinate and spongy-thickened dorsally; receptacle ciliate; corolla 15 mm long; ligule 2 mm wide; teeth 0.2–0.4 mm long; corolla tube about 6 mm long, shortly pubescent toward summit; anther tube 4.5×1.25 mm dis.; appendages 1 mm long; filaments 1 mm longer; achenes pale brown, about 6 mm long, 0.4 mm wide, the body fusiform, gradually attenuate into a beak about 2 mm long, with expanded pappus disk, narrowed at the small pale-calloused base, 10-ribbed, ribs narrow, rounded, finely spiculate; pappus pale yellow, 4–5 mm long, 2–3-seriate, about equally fine, coarsest setae about 30μ wide at base, caducous. Flowering May–June; flowers golden yellow.

Known only from the type locality.

Monomorphic.

Algeria: S.E. Oran, Sahara Atlas, near Jebel Amour, about 1500 m, Aflou, at rear of the gardens, Clary, May 8, 1888 (Alger, UCf) type; Aflou, on the left bank of the road from Sebga (Wady Sebga is northwest of Aflou), Clary 412b, in 1888 (PC) as *C. Claryi* Batt.

Relationship

Crepis Claryi appears to be closest to *C. vesicaria*, but is distinguished from that species, particularly subsp. *taraxacifolia*, which it most resembles, by the short, narrow, thick, glaucous leaves, the strongly setaceous involucre, the long appressed ventral hairs on the upper half of the inner involueral bracts, the pale brown, grad-

ually attenuate achenes, and the yellowish pappus. Some of these characteristics suggest affinity with certain species of tropical Africa, such as *C. congoensis* or *C. ugandensis*.

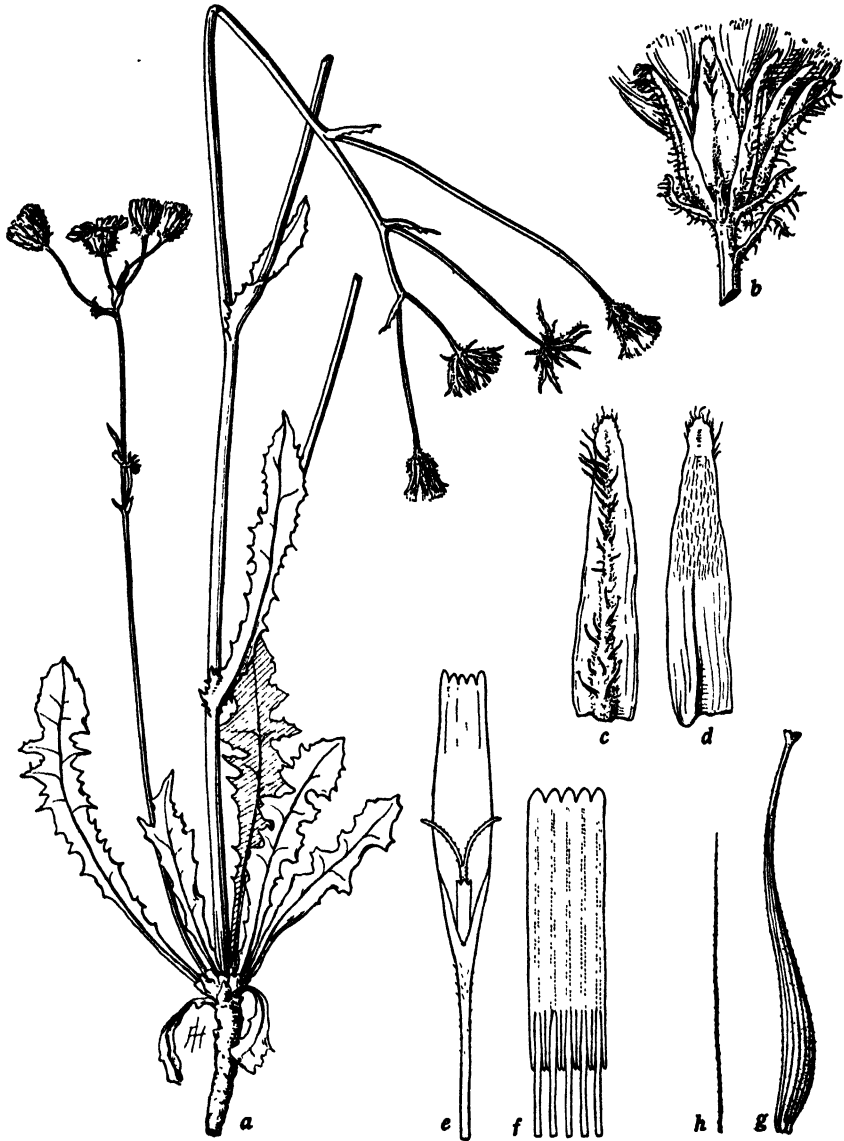


Fig. 272. *Crepis Claryi*, from type (Alger): *a*, plant, $\times \frac{1}{2}$; *b*, mature head, $\times 2$; *c*, outer and *d*, inner faces of an inner involucre bract, $\times 4$; *e*, floret lacking ovary, $\times 4$; *f*, anther tube, $\times 8$; *g*, mature achene, $\times 8$; *h*, pappus seta, $\times 8$.

181. *Crepis vesicaria* L.

Sp. Pl. 2: 805. 1753. (Pls. 30–35. Figs. 273–284.)

Perennial, biennial, or annual, 0.3–12 dm high; root slender and tapering to thick and oblong or conical, woody; caudex somewhat swollen, rarely divided; caudical leaves oblanceolate or sometimes almost spatulate or ovate, obtuse or acute, attenuate into a long or short narrowly or broadly alate petiole with broader clasping

base, sinuately or retrorsely denticulate, dentate or runcinate-pinnatifid, or pinnately or bipinnately cleft or parted, often lyrate with large truncate or hastate terminal segment, sometimes pectinate, lateral segments few or many, remote or close, pubescent on both sides with pale glandless hairs, these sometimes restricted to the veins, or glabrescent or glabrous; cauline leaves similar or sessile, middle ones lanceolate, acute or acuminate, sessile, auriculate-amplexicaul, uppermost bract-like; stem erect, branched from above or below the middle or near the base, lower branches elongated, sometimes exceeding the axis, cymosely branched near the summit, aggregate inflorescence corymbiform, or stems several, strict, arcuate or decumbent and similarly branched, stem sulcate or striate, \pm hispidulous, tomentulose, gland-pubescent or glabrescent; heads small to medium, many-flowered; involucre cylindric-campanulate in anthesis, becoming turbinate or urceolate in fruit, tomentulose or densely tomentose, often gland-pubescent or setulose; outer bracts 5–12, ovate or lanceolate, $\frac{1}{6}$ – $\frac{3}{4}$ (mostly $\frac{1}{4}$ – $\frac{1}{3}$) as long as the inner, \pm scarious; inner bracts 7–16, lanceolate, obtuse or acute, white-ciliate at the apex, appressed-pubescent on inner face, becoming dorsally carinate and spongy-thickened, fully reflexed at complete maturity; receptacle alveolate-fimbriate, fimbriae mostly low, ciliate or strigose; corolla 5.5–15 (mostly 10–13) mm long; ligules yellow, mostly reddish on outer face in marginal florets, but this sometimes absent; anther tube yellow; style branches green or yellow; achenes brown or yellowish, uniform or biform, the inner always beaked, about 10-ribbed, ribs rounded, spiculate; pappus white or tinged yellowish or dusky en masse, 3–6 mm long, exceeding the involucre, fine, soft, deciduous. Chromosomes, $2n = 8$ or 16; and a few wild plants with 9 or 12 chromosomes have been found.

Mediterranean reg. from Greece and Crete westward, W. Europe, Madeira.

This large inclusive species is extremely polymorphic. On the basis of morphology, chromosome numbers, geographic distribution, and genetical evidence, it has been found necessary to recognize 8 subspecies.

Key to the Subspecies of Crepis vesicaria

Outer involucreal bracts broadly ovate, imbricate; achenes usually biform; marginal achenes (some at least) beakless, or shortly beaked, and pale; inner achenes brown, beaked, the beak usually equal to the body.....181, *a. typica*, p. 827

Outer involucreal bracts lanceolate, not imbricate; achenes uniform or biform.

Ultimate branches (with 1 or several heads) strongly bent downward before anthesis; flowering in winter; (endemic in Sicily).....181, *b. hyemalis*, p. 833

Ultimate branches (with 1 or several heads), erect before anthesis; flowering in summer.

Heads very numerous, small, congested; involucre 6–7 mm long, 2–3.5 mm wide; corolla 5.5–7.5 mm long; achenes 3–4 mm long, biform; marginal achenes pale, obcompressed, beakless or nearly so; inner achenes brown, beaked, the beak equal to the body; (in tetraploid variants involucre 7–9 mm long; corolla 7–8 mm long; achenes 4–6 mm long); (native of W. Algeria).....181, *c. myrioccephala*, p. 836

Heads less numerous, larger, diffuse; involucre 8–13 (mostly 10–12) mm long, 4–7 mm wide; achenes 5–9 (mostly 6–8) mm long.

Achenes biform; marginal achenes 4–8 mm long, gradually and sometimes strongly attenuate to the apex, obcompressed, ventrally paler, angled, smooth or obscurely ribbed, dorsally 7-ribbed, with a small diagonal basal scar; inner achenes 4.5–9 mm long, the beak fine, about equal to the body; (native of Morocco and W. Algeria).....181, *d. stellata*, p. 838

Achenes uniform, all beaked, the marginal slightly shorter and more shortly beaked than the inner.

Achenes brown, finely beaked and ribbed, the beak smooth or muriculate; receptacle ciliate, the cilia fine, white.

Involucre shortly gland-hairy or -setulose or merely tomentose; style branches 1.5–2 mm long, green or sometimes yellow; achenes pale brown, the beak equal to the body or slightly longer; pappus white. . . . 181, *e. taraxacifolia*, p. 843

Involucre setose, the setae black, glandular or glandless, often long and conspicuous; style branches 2.5–3 mm long, dark green; achenes dark brown, the beak $\frac{1}{2}$ to $\frac{3}{8}$ of the whole achene; pappus yellowish-white; (endemic in Madeira) 181, *f. andryaloides*, p. 853

Achenes greenish or brownish-yellow, coarsely beaked and ribbed, the beak definitely ribbed and spiculate to the apex; receptacle strigose, the trichomes coarse, yellow, shining.

Involucre dark green; style branches 3 mm long, dark green; achenes greenish-yellow; (endemic in N.W. Morocco) . 181, *g. proleptica*, p. 858

Involucre pale grayish-green; style branches 2 mm long, yellow; achenes brownish-yellow; (endemic in E. Spain) 181, *h. congenita*, p. 860

181, *a. Crepis vesicaria typica* (Fiori) comb. nov. Plant annual, biennial, or sometimes perennial, 1.2–8 dm high; caudical leaves oblanceolate to ovate, up to 26 cm long, 8 cm wide (mostly 10–15 cm long, 2–3 cm wide); upper cauline leaves subtending branches of the inflorescence brown-scarious, often conspicuously vesicular, enclosing the base of the branch, sometimes lanceolate or linear or \pm swollen near base; branches 2–8-headed; peduncles 0.5–9 cm long, slender in anthesis, somewhat thickened in fruit, gland-pubescent, tomentulose, setulose or glabrescent; heads erect, small to medium, many-flowered; involucre before anthesis globose and well covered by the membranous outer bracts, in anthesis cylindric-campanulate, at full maturity turbinate, 8–14 mm high, 4–8 mm wide; outer bracts 5–12 (mostly 7–10), sometimes with 1–3 closely subtending ones, $\frac{1}{4}$ – $\frac{3}{4}$ (mostly $\frac{1}{3}$ – $\frac{2}{3}$) as long as the inner, ovate, imbricate, acute or mucronate, conspicuously brown-scarious or thinly membranous with darker median nerve, glabrous or sparsely pubescent or setulose near apex, sometimes apiculate; inner bracts 10–14, sometimes black-setulose near apex, becoming strongly rounded-carinate, spongy-thickened at base; receptacle ciliate, cilia short, white, disappearing after shedding of fruit, leaving receptacle naked; corolla about 10 mm long; ligule 1.5 mm wide, in marginal florets with or without red on outer face, rarely (cf. m.v. 12, 13) purple or brownish-red; ligule teeth 0.2–0.3 mm long; corolla tube about 3 mm long, pubescent with short stout acicular hairs; anther tube about 4×1 mm dis.; appendages 0.7 mm long, lanceolate, acute; filaments about 0.5 mm longer; style branches 2 mm long, 0.1 mm wide, green or sometimes yellow; achenes 4–8 (mostly 5–7) mm long, usually biform, but the distinctive marginal achenes sometimes absent; marginal achenes (at least some) wider and merely attenuate or very shortly beaked, flat and paler on inner face, with prominent basal callus or oblique basal scar; inner achenes terete, 0.35–0.5 mm wide, with narrow calloused base, finely beaked, beak equal to or shorter than the body, 10–12-ribbed, ribs narrow; pappus 4–5 mm long, 1–2-seriate. Flowering March–July. Chromosomes, $2n = 8, 16$. See pl. 30 and fig. 273.

Crepis macrophylla Desf., Fl. Atlan. 1: 231. 1798–1800.

C. taraxacoides Desf., loc. cit., fide Grande, Bull. Orto Bot. Nap. 8: 44. 1925 (the type of *C. taraxacoides* is lost).

C. scariosa Willd., Sp. Pl. 3: 1595. 1804.

C. raphanifolia Horn., Hafn. Add. 970. 1813; Willd., Enum. Hort. Berol. Suppl. 55. 1813.

Borkhausia purpurea Biv., Stirp. Rar. Man. 4: 22. 1813–1816.

C. purpurea Steud., Nom. Phan. 236, 1821, non Bieb.

Borkhausia leucorhodia Rehb., ex Moessl., Handb., ed. 2, 2: 1409. 1828.

C. bicolor Rehb., loc. cit.

Barkhausia Bivoniana Rehb., Fl. Exc. 1: 236. 1830-1832.

Hieraciodes vesicarium O. Kuntze, 1: 346. 1891.

C. vesicaria var. *typica* Fiori, Fl. Anal. Ital. 3: 431. 1904.

C. vesicaria subsp. *eu-vesicaria* Maire, ex Jahandiez et Maire, Cat. Pl. Maroc. 3: 851-52. 1934.

Mediterranean countries and islands from E. Thrace and Crete westward to the Balearics and E. Spain; especially in Sicily, most of Italy, and the W. Balkan Pen.; also in Lybia, Tunisia, and E. Algeria. Reported from Sardinia, but not known from Corsica. Introduced here and there in adjacent regions. Plains, hills, and lower mountains, mostly in open, sunny exposures.

The type of Linnaeus is shown in pl. 30, *a*.

Distinctive yet polymorphic, subsp. *typica* includes forms of strikingly different habit types and leaf shapes. The plant, as a general rule, develops a single erect stem which tends to branch from near the base or below the middle, the lower branches often being long and terminated by a small corymbiform cyme. Under favorable conditions, however, plants may live more than two years, at which time the caudex becomes swollen and divided, and numerous, sometimes decumbent, stems arise from the old crowns. The earliest synonym, *C. scariosa*, was distinguished by Linnaeus as var. β , merely because of its leaf shape. Although many of the leaf variations probably have a genetic basis, it would be useless for present purposes to list them all as numbered variants. Of greater significance is the tendency in certain isolated localities toward the evolution of distinct forms. This is most pronounced in the Balearic Is. and in an adjacent district in Spain, where the leaves are commonly glabrous (but not, as in Sicily, due to hybridization with a glabrous-leaved subspecies), the style branches yellow instead of green, and the outer bracts sometimes much shorter than usual. None of these characters is constant in the Balearics, however, as specimens with pubescent leaves or green style branches occur and in many plants the outer bracts are as long as usual. Thus far only 4 specimens from 2 stations in Spain have been seen by the author and, although these are uniform in the peculiar combination of characters above noted, it is at present uncertain whether the subspecies is permanently established on the mainland. For the present, therefore, it seems sufficient to record this tendency to depart from the norm of the subspecies, and merely list these variants (cf. m.v. 5, 9, 14). Certain other forms from the Balearics are known to be autotetraploids ($2n = 16$), but even this fact does not seem to warrant their recognition as subspecies (cf. m.v. 15). Tetraploid forms are also known from Sicily and Tunis which differ from the Balearic tetraploids and from each other in several respects, there being no morphological evidence that these tetraploid forms are derived from interspecific hybridization. Apparently they are local forms occurring at isolated stations. (cf. m.v. 16 and 17). It appears, therefore, that there is a general tendency toward autotetraploidy in this subspecies, and in course of time some of these forms may develop into well-marked subspecies.

This subspecies is nearest to subsp. *taraxacifolia* and subsp. *hyemalis*, with both of which it produces fertile hybrids. It is easily distinguished by the brown-scarious, ovate, imbricate outer bracts of the involucre and the similar but larger, inflated, uppermost cauline leaves, although the latter are often not so conspicuous as in fully typical forms. Also, in subsp. *typica* the marginal achenes are frequently beakless or only very shortly beaked, broader than the inner achenes, and flattened and paler on the inner face, whereas such marginal achenes do not occur in either subsp. *taraxacifolia* or subsp. *hyemalis*. This subspecies occupies a different geographic area from that of subsp. *taraxacifolia*, but the two overlap at several places, thus making possible the occurrence of intergrading forms through natural hybridi-

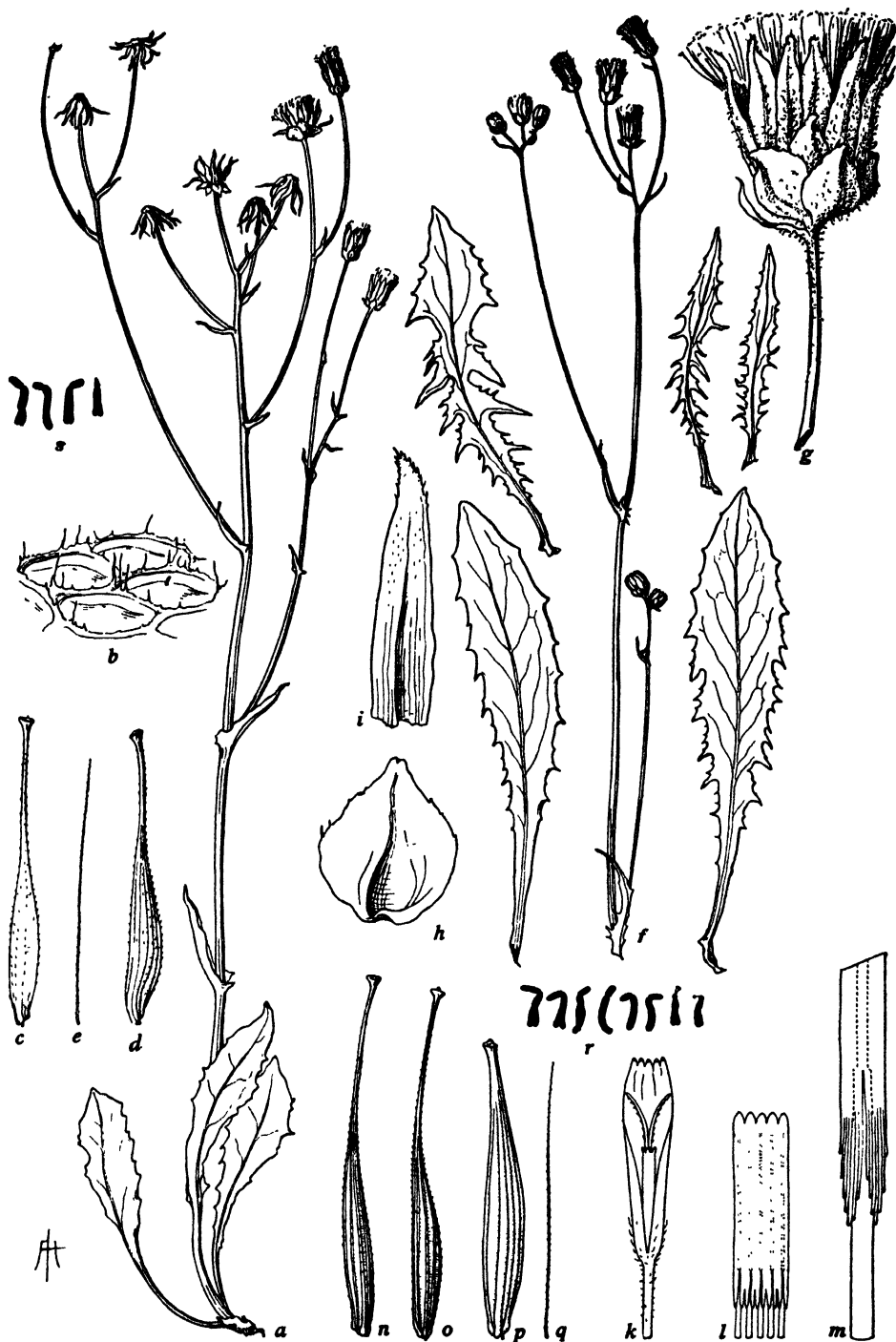


Fig. 273. *Crepis vesicaria typica*, a-e, from Gussone in 1828 (UC 259894); f-q, from hort. genet. Calif. 31.2947-1, grown from Babcock 388, a 4n form (UC 476305); r, from hort. genet. Calif. 2948 (grown from seeds collected in Majorca, near 2947, Babcock 383); s, from hort. genet. Calif. 3236 (grown from seeds collected in Tunisia by Dr. A. Eig; cf. UC 489417): a, plant, $\times ca. \frac{1}{2}$; b, detail of receptacle, $\times 25$; c-e, 2 achenes and a pappus seta, $\times 8$; f, caudex and cauline leaves and part of inflorescence, $\times \frac{1}{2}$; g, mature head, $\times 2$; h, i, outer and inner involucral bracts, inner face, $\times 4$; k, floret lacking ovary, $\times 4$; l, anther tube, $\times 8$; m, detail of appendages, $\times 32$; n-q, 1 marginal and 2 inner achenes and a pappus seta, $\times 8$; r, s, somatic chromosomes, $n = 8$ and $n = 4$, $\times 1250$.

zation (cf. m.v. 2 and 6). Natural hybrids apparently occur also between subsp. *typica* and subsp. *hyemalis* in Sicily (cf. m.v. 11 and 12).

Greece: Attica, Mt. Pentelikon, near Pikermi, *Guinardi* in 1856, *Heldr. Herb. Graec. norm.* 511 (K, B); Attica, Pikermi, *Abel* in 1912 (UWH, UWG); Attica, Athens, Minidi, *Sartorini* (B) m.v. 3; Boeotia, Onii, *Heldreich* 2262 (Bo); Achaia, Gerokomion, near Patras, *Heldreich* in 1861 (B); Macedonia, Drenovo, Mt. Radobilj, 800–900 m, *Bornmüller* 4215 (B) m.v. 2; Crete, *herb. Willd. n.* 14733–1 (BW); Crete, Canea, moist places, *Reverchon* 95 (K, Bo, Bur); Crete, between Canea and Malaxa Mts., *Babcock* 291 (UC); Crete, S. Heraclion Prov., near Tybaki, Gortyna, among ruins and rocks, marine Tertiary deposit (lime), about 413 m, *Patten* in 1900 (G). **Turkey:** Constantinople (Bo); Constantinople (?), *Aucher* 3345 in 1837 (Fl in herb. Webb). **Libya:** in *Herb. Libycae* (Genoa); Tripolitania, Tarhuna, *Pampanini* 2427 (Fl). **Tunisia:** near Sousse, *Eig* in 1930 (HU, UC); near Schott Kelbia, *Eig* in 1930 (HU); Medjex-el-Bab, *Eig* in 1930 (HU); Grombalia, *Eig* in 1930 (HU, UC) m.v. 13; Tuburbo Majus, between Zaghuan and Tebourouk, *Chabrolin* in 1931 (UC) m.v. 7; Barrage de l'Oued Kebir, *Chabrolin* in 1931 (UC) m.v. 8; Beja, *Chabrolin* in 1932 (UC) m.v. 16. **Algeria:** Bône, *Dacaine dedit* 1833 (K); near Bône, Paturagu, *Durieu* in 1840–1844, (Ms) m.v. 7 †; Kabylie, Magris Mts., 800–1000 m, *Reverchon* 247 (Ms, UWG, PC, UC); Constantine, Djebel Toumour, *Cosson* in 1853 (PC) m.v. 4; Constantine, Djebel Chilia, Aures Mts., *Cosson* in 1853 (PC) m.v. 3; Djurdjura, Mt. Tigounatin, *Maire* in 1930 (UC) m.v. 6. **Italy:** Sicily, Saline, *Gussone* in 1828 (DC, UC); Sicily, Madonie, al Cuozzo della Mufera, *Gussone* (UC) m.v. 10; Sicily, Colma Grande, Nebrodum, 1700–1800 m, *Huet du Pavillon* in 1855 (K) m.v. 10; Sicily, near Pietraperchia, *Huet du Pavillon* in 1856 (Bo); *ibid.*, 127a, b (K) b = m.v. 11; Sicily, near Palermo, Mt. Moarta, *Heldreich* in 1840 (K, Bo); Sicily, Tortorici, *Todaro* 713 (K, B, Ms); Sicily, Palermo, *Ross* 257 (K, B); Sicily, near Palermo, Segesta, *Babcock* 272, 277 (UC) m.v. 17; Sicily, Palermo, Segesta, *Bentham*, Feb.–Apr., 1847 (K) m.v. 12; S. Italy, various localities, *Gussone* (Naples); near Pozzuoli, Monte-nuovo, *Heldreich* in 1841 (K, B, BML, DS); Rome, *Woods* (K); Pisa, *Savi* in 1844 (DS); Florence, Cascine, *Joad* in 1871 (K); Modena, fields, in 1875 (Po); Modena, *Mori* in 1886 (Ms). **Switzerland:** *fide Linnaeus, loc. cit.*, *Hasselquist* (L) type. **Istria:** Fiume, *Noë* 1226 (B, K); around Dignano and on an island near Pola, *Sch. Bip. Cich.* 62 (Bur). **Dalmatia:** Salona, *Pichler* in 1868 (K, Bur); around Ragusa, *Adamovic* in 1909 (B); Perkovic, *Burnat et al.* in 1905 (Bur). **Montenegro:** Podgliva, near Trebinje, *Pantocsek* in 1872 (Bur). **Spain:** Balearic Islands, Majorca (DC); Majorca, Chateau de Belver, *Cambessedes* in 1829 (Ms); Majorca, Pont d'Inca, *Bianor-Marie* in 1917 (Bar, UC); Majorca, Mapricerinin Isle, *Font Quer* in 1920 (Bar) m.v. 5; Majorca, Miramar and St. Galderon, *Babcock* 332, 3 (UC) m.v. 15; Minorca, around Ferrarias, *Porta et Rigo* in 1885 (K) m.v. 5; Minorca, near Fornells, *Hernandez* in 1913 (Bar) m.v. 14; Minorca, Isle de Colom, *Font Quer* in 1913 (Bar); Ibiza I., St. Maten, *Font Quer* in 1920 (Bar, UC) m.v. 9; Catalonia, Eivissa, Sta. Agnes, *Gros* in 1918 (Bar, UC) m.v. 9; Eivissa, Sta. Eulalia, *Font Quer* in 1918 (Bar) m.v. 9. **France:** Var, Le Fenouillet, corkwoods, *Raine* in 1906 (G) m.v. 1.

Minor Variants of *C. vesicaria typica*

1. Stems 4, strictly erect; achenes yellowish, rather broad, shortly beaked. Plant 3 dm high; caudal leaves up to 7.5 cm long, 2.5 cm wide; cauline leaves few, linear, subamplexicaul; peduncles 1–5 cm long; involucre 10 mm long, 5 mm wide; outer bracts numerous, ovate, apiculate; florets 12 mm long; anther tube 3.5 mm long; style branches green; achenes brownish-yellow, 5.5–6 mm long, 0.6 mm wide, laterally compressed, 10-ribbed, coarsely beaked, beak about 2 mm long; pappus 4 mm long, 1-seriate. Flowering March; flowers yellow, purple on outer face of ligules. *Raine* in 1906 (G), corkwoods, La Fenouillet, Var, France.

2. The whole plant hispidulous, the stem and peduncles with scattered purple setae, those on the peduncles glandular; outer and inner involucre bracts setose near the apex, setae greenish or yellowish. *Bornmüller* 4215 (B), Drenovo, Mt. Radobilj, 800–900 m, Macedonia; *Bornmüller* 4217 (B), "Babuna," peak near "Kau-Aledipasa," Macedonia, Greece.

3. Plant low, diffusely branched from near base; leaves narrow, runcinate-pinnatifid. In habit and leaves these plants show superficial resemblance to *C. incana*. *Sartorini* (B), Athens, Minidi, Greece; *Cosson* in 1853 (PC), Aures Mts., Djebel Chilia, Constantine, Algeria; *Gussone* (PC), Sicily.

4. Very stout, with heads about twice the usual size. *Cosson* in 1853 (PC), Djebel Toumour, Constantine, Algeria.

5. Leaves glabrous, dentate, runcinate or pinnately parted; uppermost cauline leaves linear, not much inflated; outer involucre bracts with a conspicuous dark median nerve or the whole bract dark except the margin; ligules yellow, sometimes without red on outer face; style branches yellow; achenes typical. *Porta and Rigo* in 1885 (K), waysides around Ferrarias, Minorca, and

near Puigpunent, Majorca; *Rodrigues* in 1878 (Bar), Turmdent, Minorca; *Font Quer* in 1920 (Bar), Leuch, Mapricerinin Isle, Majorca, Balearic Is., Spain.

6. Plant low with several slender decumbent stems and long few-headed branches; caudical leaves small, narrow, runcinate-pinnatifid; cauline leaves mostly linear, the uppermost brown-scarious, slightly inflated; outer involucre bracts lanceolate to ovate, \pm imbricate, brown-scarious; florets about 8 mm long; anther tube about 2 mm long; style branches dark green; achenes 4–6 mm long, some marginal ones beakless, others gradually attenuate into a short beak, inner achenes gradually attenuate into a beak about equal to the body; pappus white, 2.5–4 mm long. Flowering June; flowers yellow with red on outer face of ligules. Chromosomes, $2n=9$. Probably a derivative from hybridization with subsp. *taraxacifolia*. *Maire* in 1930 (UC), meadows on calcareous soil, 1700 m, Mont Tigounatin, Djurdjura, Algeria.

7. Stems several from a strong woody root, strictly erect, few-branched; uppermost cauline leaves linear or only slightly inflated, brown-scarious; florets 5–6 mm long; anther tube 2.5 mm long; achenes 4.5–5.5 mm long, marginal ones beakless or very coarsely beaked, inner achenes abruptly attenuate into a very fine beak longer than the body; pappus white, 4.5 mm long. Flowering April; flowers yellow without red on outer face of ligules. *Chabrolin* in 1931 (UC), between Zagouhan and Tebourouk, Tuburbo Majus, Tunisia.

8. Low with large woody caudex and several robust decumbent few-branched stems; uppermost cauline leaves linear, \pm scarious; heads small to medium; peduncles and involucre densely canescent-tomentose; outer bracts with a black median nerve and, like inner bracts, a few long black bristles near the apex; florets 9 mm long; anther tube 2.5 mm long; marginal achenes 5 mm long, gradually attenuate to a beak 1 mm long; inner achenes 5.5–6.5 mm long, 0.35 mm wide, gradually attenuate into a very fine beak longer than body; pappus 4 mm long. *Chabrolin* in 1931 (UC), barrage de l'Oued Kebir, Tunisia.

9. Leaves glabrous with ciliate margins; caudical leaves remotely pinnately parted, terminal segment rather small, lateral segments mostly opposite, oblong-acute; uppermost cauline leaves linear, brown-scarious; outer involucre bracts $\frac{1}{4}$ as long as inner bracts; style branches yellow; marginal achenes 5 mm long, gradually attenuate into a coarse beak 1 mm long; inner achenes 5 mm long, abruptly attenuate into a fine beak equal to body; pappus 4 mm long. Flowering May; flowers yellow with red on outer face of ligules. The plants from the three localities given below are so similar that it seems likely that this form is adventive on the mainland, but how extensive is its occurrence there is not known. *Font Quer* in 1920 (Bar, UC), San Maten, Ibiza I., Balearic Is.; *Gros* in 1918 (Bar, UC), a la Cala de les Forretes, Sta. Agnes, Eivissa; *Font Quer* in 1918 (Bar), riera de Sta. Eulalia, Eivissa, Catalonia, Spain.

10. Rather low plants (1.6–3 dm high); caudex perennial, woody, simple or 1-divided; stem slender with 1–2 branches from near base and 2–3 higher up; branches 1–2-headed, the whole plant bearing only 4–6 heads; caudical leaves small, shortly petioled, runcinate-pinnatifid, terminal segment small, lateral segments close, acute, dentate; uppermost cauline leaves linear or slightly inflated, brown-scarious; style branches yellow or greenish; achenes 6–7 mm long, slender, gradually attenuate into a beak shorter than the body, marginal ones not much different from inner ones; pappus 4 mm long. Flowering June; flowers yellow with red on outer face of ligules. Gussone's plants, cited below, were taken from his own specimens, determined as *C. praecox* Balb., but this name is a synonym of *C. nicaeensis* Balb. (q.v.) Gussone (UC ex Herb. Neapol.), al Cuozzo della Mufera, Madonie, Sicily; *Huet du Pavillon* in 1855 (K), among tall herbs, Nebrodum, Colma Grande, 1700–1800 m, Sicily.

11. Aggregate inflorescence atypical; stem 2 dm high, 3-branched near summit, branches 4–6 cm long, pedunculate, notably thickened near base of head, stem and branches gland-setulose, setules yellow near base of stem, black above, shorter on peduncles; uppermost cauline leaves linear, green; outer involucre bracts lanceolate to ovate, with broad scarious margins, a median black nerve, and, like inner bracts, a median row of short black setae; florets 10 mm long, yellow with red on outer face of ligules; achenes 7 mm long, gradually attenuate into a beak equal to or shorter than body; pappus white, 4–6 mm long. Flowering May. Very probably an extreme variant occurring among hybrid forms resulting from natural hybridization between this subspecies and subsp. *hyemalis* (cf. m.v. 12). *Huet du Pavillon* 127b in 1856 (K), among herbs on clayey soil near Pietraperasia, Sicily.

12. Caudex, habit of plant, and leaf shape more like those of subsp. *hyemalis*; leaves mostly pubescent, sometimes glabrous; uppermost cauline leaves linear to broadly lanceolate, \pm scarious; heads medium to large; outer involucre bracts varying from broadly lanceolate to ovate, brown-scarious; like inner bracts, mostly devoid of black bristles; florets varying from yellow to purple; achenes sometimes more slender, like those of subsp. *typica*, sometimes broader, like subsp. *hyemalis*; marginal achenes sometimes like those of subsp. *hyemalis*, sometimes like subsp. *typica*; pappus 4–6 mm long. Flowering Feb.–June. There are undoubtedly hybrid forms between the two subspecies. Based upon the fact that F₁ hybrids between subsp. *typica* and subsp. *taraxacifolia*

are known to be highly fertile and upon the fact that subsp. *hyemalis* is closely related to these two subspecies, the more extreme variant described as m.v. 11 indicates that further field work may reveal the occurrence of still other intergrading forms. The specimens of Fiori, Béguinot, and Pampanini distributed by Fiori in Fl. Ital. Exsic. no. 999 are partly *C. hyemalis* (q.v.) and partly variants, like those cited here. *Fiori, Béguinot, and Pampanini 999* (K, 3 specimens on one sheet; BML, 2 specimens), among herbs on clayey soil, 300 m, near Agrigentum (Girgenti), Sicily; *Lacaita 69/06* (BML), among herbs on calcareous soil, San Martino (Palmero) Sicily; *Lacaita 178/07* (BML), meadows, 1100 m, Monte Pizzuta, alla Portella di Xirovuddi, Sicily; *Klatt* (G), among herbs in fields, Palermo, Sicily; *Benthams* (K), Segesta, near Palermo, Sicily.

13. In leaf shape and habit this variant resembles *C. Clausonis*; taproot straight, stout, woody, not forked, like *C. Clausonis*; caudex much divided; caudical leaves numerous, short, erect, oblanceolate, acute, denticulate, glabrous, margins ciliate; stems several, 1.5–2 dm high, semi-decumbent, branches 1–4-headed; uppermost cauline leaves lance-linear, \pm brown-scarious; heads erect, medium; outer involucre bracts ovate, imbricate, brown-scarious; florets short, yellow, deep reddish-purple on outer face of ligules; marginal achenes 4 mm long, 0.5 mm wide, gradually attenuate into a short coarse beak, flat and paler on inner face; inner achenes 4–5 mm long, abruptly attenuate into a fine beak equal to body; pappus 4 mm long. Flowering March. *Eig* in 1930 (UC), wheat fields, Grombalia, Tunisia.

14. Unique in habit of inflorescence and a peculiar combination of characters; annual (!); caudical and lower cauline leaves up to 28 cm long, 6 cm wide, spatulate, with very long narrow petiole with much broadened clasping base, irregularly retrorsely dentate or runcinate, glabrous; stem 7 dm high, erect, stout, branched from below middle; branches long, mostly unbranched, except at summit, where is borne an umbel of 10–13 heads, the peduncles subtended by ovate-lanceolate, brown-scarious bracts; peduncles 1–2 cm long, slender; heads erect, rather small, many-flowered; florets 7 mm long; anther tube 2 mm long; style branches yellow; achenes 4–5 mm long, the marginal narrow, gradually attenuate, not beaked, ventrally flat and paler, the inner gradually attenuate into a fine beak shorter than the body; pappus 3.5 mm long. Flowering June; flowers yellow, without red on outer face of ligules. This peculiar plant may exemplify an extreme manifestation of the tendency already noted in this species and found in the Balearics, to develop distinct forms (cf. m.v. 5 and 9). *Hernandez* (Bar), near Fornells, Minorca, Balearic Is., Spain.

15. Tall, robust annuals; caudical leaves variable, often like those in typical forms, sometimes much longer and wider, dentate to bipinnate; upper cauline leaves lance-linear, the uppermost brown-scarious; outer involucre bracts $\frac{1}{2}$ as long as the inner, imbricate, ovate, acute or apiculate, membranous; corolla 9–11 mm long, yellow; ligule purplish-red on outer face; anther tube 3.5 mm long; style branches green or yellow; marginal achenes equal to inner achenes and similarly beaked, or sometimes shorter, not beaked, ventrally flat and pale, dorsally convex and ribbed; inner achenes 6–7 mm long, subterete, 0.4–0.5 mm wide, gradually attenuate into a delicate beak equal to body; pappus 4–5 mm long. Flowering July. Chromosomes of progeny, $2n = 16$. Much reduced plants of this variant were collected along the stony trail in Barañica de Soller at 500–600 m alt., *Babcock 378, 379* (UC). As these plants were low and diffusely branched from the base, they were at first mistaken for another species. Their garden progeny, however, were typical of this variant and were tetraploids. *Babcock 382* ex hort. genet. Calif. 31.2947–1, 2 (UC), seed collected along steps of retaining wall in olive orchard near house, Miramar; *Babcock 383* ex hort. genet. Calif. 31.2948–1, 5, 9 (UC), seed collected in olive orchard, St. Galderon, between Miramar and Valdemosa, Majorca, Balearic Is.

16. Caudex and stem very robust; leaves long, up to 22 cm, long-petioled; uppermost cauline leaves ovate-lanceolate, brown-scarious; heads large, many-flowered; outer involucre bracts $\frac{1}{2}$ as long as inner bracts, broadly ovate, imbricate, glabrous, black-apiculate; corolla 10 mm long, yellow; ligule purplish-red on outer face; marginal achenes 5 mm long, 0.75 mm wide, ventrally straight, slightly beveled and faintly ribbed, dorsally convex, strongly ribbed, strongly attenuate or shortly and coarsely beaked; inner achenes 5.5–6 mm long, 0.5 mm wide, delicately beaked, beak equal to body; pappus 4–5 mm long. Flowering April. Chromosomes of progeny, $2n = 16$. Only the one plant cited here has been collected. If it represents a considerable population at that station, this may be the beginning of a distinct subspecies. *Chabrolin* in 1932 (UC), Béja, southwest of Mateur and southeast of Tabarca, N. Tunisia.

17. Caudex and stem very robust; leaves extremely variable, often very broad, sometimes bipinnate; uppermost cauline leaves lanceolate, \pm inflated near base, brown-scarious; heads large, many-flowered; outer involucre bracts $\frac{1}{3}$ – $\frac{1}{2}$ as long as inner bracts, imbricate, ovate, acute or apiculate, membranous; corolla 9 mm long, yellow; ligule purplish-red on outer face; anther tube 3–3.5 mm long; style branches yellow or pale green; marginal achenes 4.5–5.5 mm long, ventrally straight and flat or beveled, dorsally convex, strongly attenuate or shortly and coarsely beaked, strongly ribbed; inner achenes 5–6 mm long, finely beaked, beak equal to or longer than body;

pappus 4–5 mm long. Flowering May. Chromosomes of progeny, $2n = 16$. The more striking variations in leaf size have occurred among cultivated progeny. The indigenous plants seen by the author were mostly dried up. Additional material and especially field observations are needed in order that satisfactory comparison of indigenous plants of this tetraploid population may be made with typical diploid plants of the subspecies. *Babcock* 272, 274, 275, 276, 277 (UC), near Greek temple, Segesta, Palermo; *Babcock* 278, 279, 280 (UC), among ruins, Greek theatre, Segesta, Palermo, Sicily.

181, *b. Crepis vesicaria hyemalis* (Biv.) Babc., Univ. Calif. Publ. Bot. 19: 404. 1941. Plant 1.3–3.9 dm high; caudex woody, perennial; caudical leaves oblanceolate to spatulate, up to 17 cm long, 4.5 cm wide; upper cauline leaves linear, bractlike; branches 2–5-headed, the very young branches and peduncles strongly bent downward before anthesis; peduncles 1–10 cm long, rather stout, tomentose, setose, the setae black, glandular or glandless; heads erect in anthesis, medium, many-flowered; involucre cylindric-campanulate, becoming urceolate or turbinate, at maturity 10–13 mm long, 5–7 mm wide; outer bracts 6–9, about $\frac{1}{3}$ as long as the inner, lanceolate or narrowly ovate, acute, tomentose, with a median row of black glandless setae; inner bracts 11–15, with black setae longest near the apex, becoming broadly carinate, spongy-thickened at base; receptacle ciliate, cilia short, white; corolla 12–13 mm long; ligule 1.5 mm wide, in marginal florets with red on outer face; corolla tube about 4 mm long, pubescent with acicular hairs 0.1–0.35 mm long; anther tube 3.5×1 mm dis.; appendages 0.7 mm long, narrow, acute; filaments 0.6 mm longer; style branches 2 mm long, 0.1 mm wide, green; achenes uniform, pale brown, 5–7 mm long, 0.5 mm wide, subterete, narrowed at the calloused hollow base, attenuate into a fine or rather strong beak nearly equal to the body, 10-ribbed, the ribs prominent; pappus 6 mm long, 2-seriate. Flowering Nov.–March. Chromosomes, $2n = 8$. See fig. 274.

Barkhausia hyemalis Biv., Stirp. Rar. Sic. Man. 1: 6. t. 2. 1813; Rehb., Pl. Crit. 1: 36. t. 40. f. 83. 1823.

Lagoseris taraxacoides Rehb., Pl. Crit. 1: 28. t. 29. 1823.

B. taraxacifolia var. *hiemalis* DC., Prod. 7: 154. 1838 excl. syn. *p.p.*

Crepis taraxacoides Guss., Fl. Sic. 2: 410. 1843, non Desf.

Heraciodes hiemale O. Kuntze, Gen. 1: 346. 1891.

Sicily, endemic. It has been reported to occur in "Sicily and the Peninsula," but no specimens from the mainland have been seen by the writer. In herb. DC. Prod., vii. 154 n. 11 is a specimen collected by Thomas in Sardinia in 1828 which may be this species. Type locality, around Palermo. Gussone (*loc. cit.*) lists stations distributed throughout the island, mostly near the coast, but three in the higher district west of Etna. At a centrally located station, hybrid forms were collected (cf. m.v. 18, 19). It appears, therefore, that this subspecies has been fairly common in Sicily. But until careful field studies are made, it will remain uncertain how extensively the subspecies is maintaining itself true to type, there being very clear evidence that it hybridizes naturally with subsp. *typica*, producing a wide range of intergrading forms. Examples of these are cited below as numbered variants, but, also, cf. subsp. *typica* m.v. 12.

In lieu of an authentic specimen of Bivona-Bernardi, his illustration (*loc. cit.*) has been reproduced in fig. 274, *a*. His drawing agrees well with his description, showing the thick root and distinctive basal and cauline leaves. His illustration features only one type of achene, and that is definitely beaked. The achenes on Fiori's specimens (Fl. Ital. exsic. 999) which are typical of this species agree with Bivona's figure very closely. Fiori's specimens, distributed under number 999b, lack mature fruits. In addition to the specimens cited below, five sheets, probably Gussone's material, in Herb. Ist. Orto Bot. Napoli, have been seen by me. They exhibit con-

siderable variation in leaf shape, but all have typical heads and involucre, and in specimens with fruits these are typical.

This subspecies is distinct from all other woody-based perennial species except *C. Clausonis* in its truly winter-flowering habit. From *C. Clausonis* it is distinct in many details of the leaves and flowers, in the pubescence of the involucre, and in the habit of growth. From *C. spathulata* it is well set off by the broader setose involucre, the larger and more finely beaked achenes, as well as by leaf shape and other characters. Its closest relatives are subspp. *typica* and *taraxacifolia*. Its perennial habit and somewhat larger heads indicate that subsp. *hyemalis* is somewhat more primitive than subsp. *typica* and subsp. *taraxacifolia*, and in this respect it is comparable to subsp. *andryaloides*. It is sufficiently similar to subsp. *typica* genetically so that it hybridizes freely with that subspecies in nature, producing numerous intermediate forms which may be found difficult to classify. Careful field studies are needed to determine the present status of this subspecies in Sicily and the possible establishment of new constant types resulting from hybridization between it and subsp. *typica*.

Sicily: Palermo, Mt. Pellegrino, near Semaforo, 500 m, *Fiori, Béguinot, and Pampanini* in 1906, Fl. Ital. Exsic. 999b (G, K, Bur, BML); *ibid.*, *J. Ball* in 1853 (G); Palermo, fields, *Ross* in 1894 (G); *ibid.*, *Ross* in 1901 (Po); Girgenti, 300 m, *Fiori, Béguinot, and Pampanini* in 1906, Fl. Ital. Exsic. 999 (G, K, Bur, Co) certain specimens in this widely distributed collection are variants, probably derived from hybridization with subsp. *typica* (cf. m.v. 12); Caltanisetta, low open places, *Ross 744a, b* in 1905 (G) *a* = m.v. 18, *b* = m.v. 19; Palermo, San Martino, *Lacaita 69/06a, b, c* (BML) *a* = m.v. 20, *b* and *c* = m.v. 21; Palermo, fields, *Todaro 1000c, d* (K) m.v. 24; Palermo, *Lanza* in 1931 (UC) m.v. 25, 26.

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18. Resembles subsp. *typica* as follows: plant 4 dm high; stem erect, branches strict, cymosely branched at summit, branches pedunculate, erect before anthesis; but leaves, heads, and involucral bracts are more like those of subsp. *hyemalis*; leaves pubescent; achenes intermediate; pappus 4–5 mm long. *Ross 744a* (G), Caltanisetta, Sicily.

19. Stems 2.4 dm high, slender, erect, leafy, branched at summit; leaf shape more like that of subsp. *hyemalis*, leaves pubescent; involucral bracts like those of *hyemalis*; achenes 4 mm long, intermediate in shape; pappus 3 mm long. *Ross 744b* (G), Caltanisetta, Sicily.

20. Stem erect, cymosely branched above the middle; leaves glabrous; heads intermediate, bracts like those of subsp. *hyemalis*; achenes 4 mm long, intermediate; pappus 4–5 mm long. *Lacaita 69/06a* (BML), San Martino, Palermo, Sicily.

21. Stem erect, paniculately branched from near base or above middle, branches strict; leaves and heads more like those of subsp. *hyemalis*, leaves pubescent; achenes 4–5 mm long, intermediate; pappus 4 mm long. *Lacaita 69/06b, c* (BML), San Martino, Palermo, Sicily.

22. Stem very slender, semierect, branched near summit; leaves intermediate in shape, glabrous; heads small, more like those of subsp. *typica*; involucre shortly gland-pubescent, black setae absent; outer involucral bracts lanceolate, brown-scarious; achenes all finely beaked, 6 mm long; pappus 4–5 mm long. *J. Ball* in 1853a (K), Mt. Pellegrino, Palermo, Sicily.

23. Leaves more like those of subsp. *typica*, pubescent; stem erect, branched from near base, branches elongated, paniculately branched, few-headed; young branches erect before anthesis; heads intermediate in size; outer involucral bracts lanceolate, gland-pubescent; inner bracts tomentose, gland-pubescent, ± black-setose; corolla 10–11 mm long; corolla tube 3 mm long, densely pubescent; anther tube 3.5 × 1 mm dis., appendages 0.6 mm long, acute; style branches 2 mm long, green; achenes 5–6 mm long, all slender-beaked; pappus 4–5 mm long. *J. Ball* in 1853b, c (K), Mt. Pellegrino, Palermo, Sicily.

24. Habit like that of subsp. *typica*; leaves intermediate, glabrous or pubescent; stem erect, branched from near base, branches long, branched near summit; heads like those of subsp. *hyemalis*; achenes 5–6 mm long, all slender-beaked; pappus 4–5 mm long. On same sheet with these are two diminutive specimens of subsp. *typica*. *Todaro 1000c, d* (K), Palermo, Sicily.

25. Habit like that of subsp. *typica*; stem erect, remotely branched from near base to summit, branches cymosely branched near summit; leaves oblanceolate, up to 9 cm long, 1.5 cm wide, retrorsely pinnately parted, lateral segments close, gradually diminishing to the stout petiole, glabrescent; uppermost cauline leaves linear, not scarious; heads like those of subsp. *hyemalis*;



Fig. 274. *Crepis vesicaria hyemalis*, *h*, from original figure of Bivona-Bernardi; *b-g*, from Fiori et al. 999b (G); *h-m*, from Ross 41 (G); *n-p*, from Fiori et al. 999 (G); *q*, from hort. genet. Calif. 2053 (grown from seed received from Professor D. Lanza, Palermo, Sicily; cf. UC 517914): *a*, plant, \times ca. 1; *b*, plant, \times 1; *c*, head, \times 2; *d*, inner involucral bract, \times 4; *e*, floret lacking ovary, \times 4; *e'*, detail of ligule teeth, \times 50; *f*, anther tube, \times 8; *g*, detail of appendages, \times 32; *h*, branch, \times 1; *k-m*, marginal and inner achenes and a pappus seta, \times 8; *n*, *o*, marginal and inner achenes, \times 8; *p*, detail of receptacle, \times 20; *q*, somatic chromosomes, $n = 4$, \times 1250.

achenes 5–6 mm long, all slender-beaked; pappus 3.5–4 mm long. *Lansa* in 1931 (seed) plant ex hort. genet. Calif. 32.3053–10 (UC), Palermo, Sicily.

26. Habit like that of subsp. *typica*; stem erect, strictly branched, branches corymbiform; leaves oblanceolate, lyrate pinnately parted, terminal segment oblong, sagittate, lateral segments remote, lanceolate, dentate, gradually diminishing to the narrow petiole, segments and rachis densely pubescent with pale glandless hairs; heads like those of subsp. *hyemalis* but small; achenes 5–6 mm long, all slender-beaked; pappus 3–4 mm long. *Lansa* in 1931 (seed) plant ex hort. genet. Calif. 32.3058–8 (UC), Palermo, Sicily.

181. *c. Crepis vesicaria myriocephala* (Coss. et Durieu) Babc., Univ. Calif. Publ. Bot. 19: 404. 1941. Plant 5–10 dm high; caudex woody, biennial or perennial; caudical leaves oblanceolate to spatulate, denticulate or dentate, up to 30 cm long, 3 cm wide; upper cauline leaves lanceolate, acuminate, auriculate-amplexicaul; branches elongated, much branched near the summit, forming congested many-headed corymbiform cymes; peduncles 0.5–1.8 cm long, slender; heads erect, small, 20–30-flowered; involucre cylindric-campanulate, 6–7 mm long, 2–3.5 mm wide; outer bracts 5–6, about $\frac{1}{4}$ as long as the inner, ovate-lanceolate to lance-linear, becoming brown-scarious, lax and sometimes narrowly carinate; inner bracts 7–8, becoming strongly carinate, spongy-thickened; receptacle ciliate, cilia short, fine, white; corolla 5.5–7.5 mm long; ligule 0.8–1 mm wide, with or without a median red stripe on outer face; corolla tube 1.5–2.75 mm long, pubescent with acicular hairs up to 1 mm long; anther tube (2) 2.5×0.8 mm dis.; appendages 0.5 mm long, acute; filaments 0.5 mm longer; style branches 1–1.5 mm long, 0.1 mm wide, green; achenes 3–4 mm long, biform; marginal achenes gradually attenuate to the apex, scarcely or not at all beaked, laterally compressed, ventrally straight, nearly smooth, pale yellow, dorsally curved, tawny, more definitely ribbed, with small oblique scar near base; inner achenes pale or deep tawny, terete, constricted above the narrow pale-calloused base, abruptly attenuate into a fine beak equal to body, 10-ribbed, ribs fine; pappus 3–3.5 mm long, 2-seriate. Flowering Jan.–June. Chromosomes, $2n = 8, 16$. See pl. 31 and fig. 275.

Crepis floribunda Pomel, Nouv. Mat. Fl. Atl. 2: 260–261. 1875.

C. vesicaria var. *myriocephala* (Coss. et Durieu) Maire, ex Jahandiez et Maire, Cat. Pl. Maroc. 3: 851–852. 1934.

Algeria, throughout the Tell Atlas (Little Atlas) from the Mitidja, near Algiers, westward; hills and plains; occasional and sometimes abundant locally. The W., E., and S. limits are not definitely known.

This very distinct subspecies is closely related to subsp. *taraxacifolia*. As a result of natural hybrids occurring between the two, which are at least partly fertile, intermediate forms are found, some of which are difficult to classify (cf. m.v. 27, 29). Autotetraploid forms also occur; for example, m.v. 30, which differs from typical subsp. *myriocephala* only in somewhat larger size, especially of the heads, florets, and fruits, but resembles subsp. *myriocephala* in the very numerous, congested heads and the large, spatulate, nearly entire caudical leaves.

The specimen of Cosson, collected in 1852, in herb. Cosson, which is labeled *Barkhausia myriocephala*, may be considered the type.

Algeria: Alger Prov., near Mascara, Plaine d'Eghris, *Cosson* in 1852 (PC, type, K); Alger, Gué de Constantine, *Cosson* in 1875 (K, Bo) m.v. 28; Alger, Mitidja Plain, *Babcock* 260, 261 (UC); Alger, Mustapha superieur, *Paris* 101 (G, Mo) m.v. 28; Alger, *Trabut* in 1920 (UC) m.v. 29; Alger, between Hamam Rijha and Marguerite, *Babcock* 264a, b (UC) m.v. 30; Oran Prov., *Durieu* in 1846 (PC); Oran, near Sidi bel Abbès, *Warion* in 1873 (P, K, Bo, Ms, G, UCf); Oran, l'Habra, *Pomel* (UC) m.v. 27. **France** (adventive): Bruyère de Serres, ex herb. Gaudefroy (K) m.v. 29.

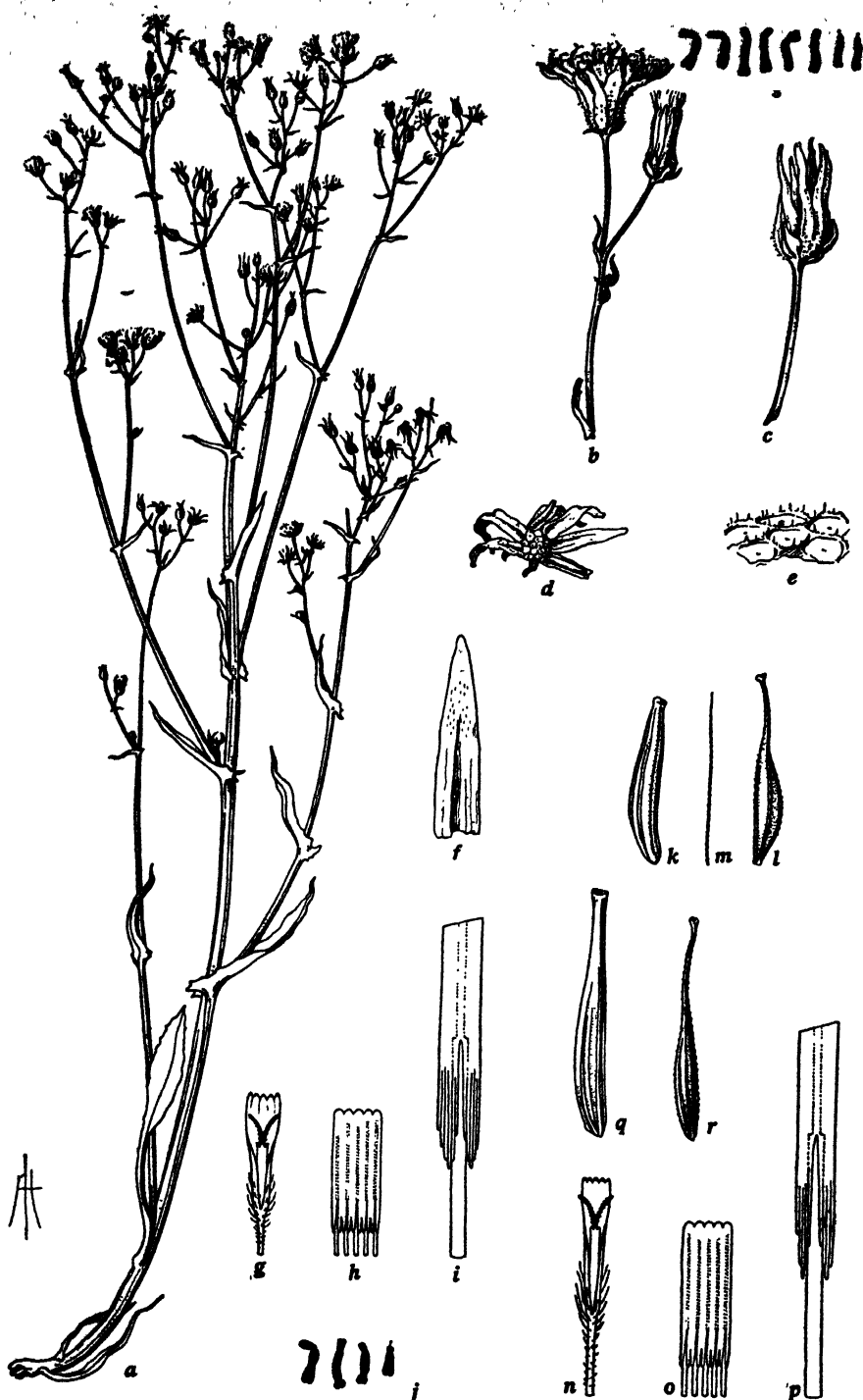


Fig. 275. *Crepis vesicaria myriocephala*, a-m, from Babcock 260 (UC 429448); n-p, from Warion in 1873 (G); q, r, from Babcock 261 (UC 429447); s, from hort. genet. Calif. 2944, Babcock 264 (cf. UC 429444): a, basal branch, $\times \frac{1}{2}$; b-d, heads, $\times 2$; e, detail of receptacle, $\times 25$; f, outer involucre bract, inner face, $\times 4$; g, floret lacking ovary, $\times 4$; h, anther tube, $\times 8$; i, detail of appendages, $\times 32$; j, somatic chromosomes, $n = 4$, $\times 1250$; k-m, marginal and inner achenes and a pappus seta, $\times 8$; n, floret lacking ovary, $\times 8$; o, anther tube, $\times 8$; p, detail of appendages, $\times 32$; q, r, marginal and inner achenes, $2n = 16$ ($x = 4$), $\times 1250$.

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27. (*C. floribunda* Pomel, *loc. cit.*) Since the specimen at hand (ex Herb. Univ. d'Alger) is fragmentary, Pomel's complete description, translated from the French, is here given: "Heads very numerous in a corymb with short slender peduncles. Involucre few-flowered, bracts few, strongly carinate at maturity; outer bracts lanceolate, lax, scarious at margin; (inner) bracts herbaceous, linear. Achenes small, the marginal very shortly beaked, the others gradually attenuate into a fine beak $\frac{1}{3}$ the length of the whole achene. Receptacle fimbriate. Lower leaves attenuate into a petiole, oblong lanceolate, unequally dentate or pinnatifid-lyrate; cauline leaves sessile, rounded amplexicaul, lanceolate or linear. Stem erect, branched, branches fastigiate; root perennial, vertical. Plant more or less pubescent or hispidulous. Flowering Apr.-May. Fertile fields: Mitidja (Alger), vallee du Chelif (Alger-Oran), plaine du Tlelat (Oran), Oued Saidia (prov. ?)." The lyrate, pinnately parted caudical leaves and dense gland-pubescent of upper stem and leaves, peduncles, and involucre characterize this as a distinct form with florets, style branches, achenes, and pappus closely similar to typical subsp. *myriocephala*. It may have resulted from natural hybridization between this subspecies and subsp. *taraxacifolia*. Pomel (UC), L'Habra, Oran, Algeria.

28. Heads fewer and somewhat larger than in typical subsp. *myriocephala*; involucre in most of the plants densely setose with short black glandless setae. Perennial, 3-4.5 dm high; root, leaves, stem, and habit typical; heads in small congested corymbs; involucre canescent-tomentose, hispid with short black setae; outer bracts 5-6, lanceolate, $\frac{1}{3}$ as long as the inner; inner bracts 8-10, dorsally carinate; corolla 7 mm long; ligule yellow with or without dorsal red stripe; style branches green; achenes 3.5-4 mm long, both marginal and inner forms typical; pappus 2.5-4 mm long. Flowering Feb.-July. These plants may show the effects of natural hybridization between this subspecies and subsp. *taraxacifolia*. Cosson in 1875 (K, Bo) Gué de Constantine, Alger, Algeria; Paris 101 (G, Mo), moist fields, Mustapha superieur, Alger, Algeria; *Bové 205* (MW), "Mauritania" (includes Algeria).

29. Caudex elongated, 2-4-furcate; stems several, slender, erect or arcuate near base, 2.5-3.5 dm high; heads less numerous than in typical forms, sometimes slightly larger. Otherwise typical of subsp. *myriocephala*. Possibly old plants which have become somewhat weak. The specimen in Herb. Berol. from Blida (cited below) was wrongly identified by me in 1925 as a subspecies of *C. amplexifolia*. Trabut in 1920 (UC), Alger, Algeria; collected April 26, 1840 (B, UCf), Blida, Mitidja, Algeria; ex herb. Gaudefroy (K, UC), Bruy're des Serres, near Paris, France (probably adventive).

30. Branches more robust, spreading, making the diameter of the whole plant greater than typical plants of comparable height; upper stem, branches, and peduncles \pm hispidulous; involucre 7-9 mm long, finely setose or merely tomentulose; corolla 7-8 mm long; style branches green; achenes 4-6 mm long, marginal ones not beaked or with a very short beak, inner ones gradually attenuate into a beak somewhat coarser than in typical forms; pappus 4-4.5 mm long. Flowering May-June. Garden plants grown from seed collected from wild plants were much more robust than their parents, with caudical leaves up to 40 cm long and 7 cm wide. But in these garden plants both caudical and cauline leaves were typical of subsp. *myriocephala* in shape; there was no evidence of previous hybridization with subsp. *taraxacifolia*; and, except for the slightly larger heads, florets, and achenes, these plants would pass for subsp. *myriocephala*. Three of these garden plants had $2n=16$ chromosomes. Therefore, it is practically certain that the two wild plants cited below are a tetraploid form of this subspecies. There was some variability in size and in time of flowering among the cultivated progeny, but typical diploid plants are variable in these respects also. Ex hort. genet. Calif. 31.2844-9 (UC), cult. from seeds taken from the following: *Babcock 264a, b* (UC), route Alger-Oran, between Hamam Rijha and Marguerite, Algeria.

181, *d. Crepis vesicaria stellata* (Ball) Bab., Univ. Calif. Publ. Bot. 19: 404. 1941. Plant 1-12 dm high; root woody; caudex 0.5-2 cm wide; caudical leaves oblanceolate, dentate to lyrate pinnately parted, up to 35 cm long, 6 cm wide; upper cauline leaves lanceolate, acute or acuminate, auriculate-amplexicaul, uppermost bractlike; branches elongated, few-headed, the aggregate inflorescence open, corymbiform; peduncles 0.8-7 cm long, slender, little changed in fruit; heads erect, medium, many-flowered; involucre cylindric-campanulate, 8-12 (mostly 9-11) mm long, 4-6 mm wide, sometimes hispid with short black or long greenish hairs with or without glands; outer bracts about 10, lanceolate, acute, about $\frac{1}{3}$ as long as the inner, becoming lax, scarious, and sometimes narrowly carinate; inner bracts 8-14, strongly carinate in fruit, half enclosing the marginal achenes, becoming spongy-

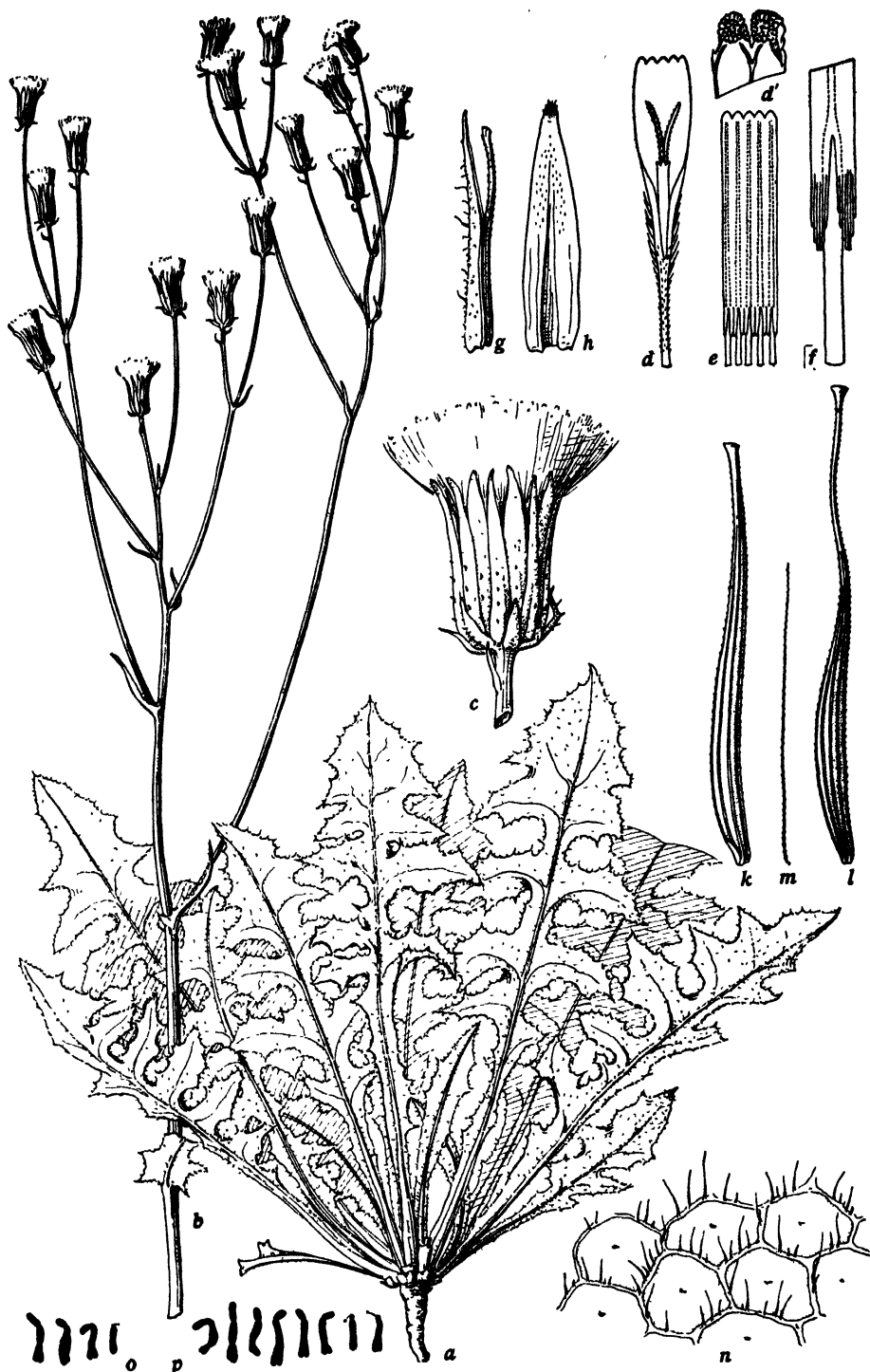


Fig. 276. *Crepis vesicaria stellata*, a-n, from type (B); o, from hort. genet. Calif. 2847, Babcock 267 (cf. UC 429439); p, from hort. genet. Calif. 3473, Maire et Wilczek 201 (cf. UC 632071): a, basal part, $\times \frac{1}{2}$; b, upper stem and inflorescence, $\times \frac{1}{2}$; c, fruiting head, $\times 2$; d, floret lacking ovary, $\times 4$; d', detail of ligule teeth, $\times 50$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, inner involucre bract enclosing achene, $\times 4$; h, inner bract, inner face, $\times 4$; i, achenes and pappus setae, $\times 8$; n, detail of receptacle, $\times 25$; o, somatic chromosomes, $n = 4$, $\times 1250$; p, somatic chromosomes, $2n = 16$ ($x = 4$), $\times 1250$.

thickened at base; receptacle ciliate, cilia white, 0.3–0.5 mm long; corolla 10–11 mm long; ligule 1 mm wide, purplish-red on outer face; corolla tube 3–4 mm long, pubescent with acicular hairs up to 0.7 mm long; anther tube (3)4 × 1 mm dia.; appendages 0.5 mm long, oblong, acute; filaments 0.5 mm longer; style branches 2–2.5 mm long, 0.1 mm wide, green; achenes biform, variable in size; marginal achenes 4–8 mm long, gradually but sometimes strongly attenuate to the apex, obcompressed, ventrally paler, angled, smooth or obscurely ribbed, dorsally 7-ribbed, with small diagonal basal scar; inner achenes 4.5–9 mm long, pale brown or tawny, 10-ribbed, the beak usually equal to the body, rarely (cf. m.v. 40) much shorter; pappus 4–5 mm long, 2-seriate. Flowering April–July. Chromosomes, $2n = 8, 9, 12, 16$. See fig. 276.

Crepis taraxacifolia subsp. *stellata* Ball, Jour. Bot. n.s. 2: 371. 1873.

C. hirsuta Pomel, Nouv. Mat. Fl. Atlan. 2: 260, et nota 261. 1875.

C. vesicaria var. *stellata* (Ball) Maire, ex Jahandiez et Maire, Cat. Pl. Maroc. 3: 851–852. 1934.

C. taraxacifolia var. *tangerina* Pau, Mem. R. Soc. Esp. Hist. Nat. 12: 351. 1924.

C. vesicaria var. *tangerina* (Pau) Maire, ex Jahandiez et Maire, loc. cit.

C. taraxacifolia var. *sulphurea* Maire et Wilczek, ex Maire, Contr. no. 2075 (Fl. Anti-Atlas).

Morocco and W. Algeria, mostly in mountainous country; it has been collected at only two coastal points; plains, hills, mountain valleys, and rocky slopes.

This subspecies apparently ranges farther south in Morocco than subsp. *taraxacifolia*. At the same time, the N. and E. limits of its range include the areas occupied by both subsp. *taraxacifolia* and subsp. *myriocephala*; and, since it possesses characters derived from both these subspecies, they are its nearest relatives. Plants of this subspecies with 8 and 16 chromosomes and others with intermediate numbers occur, which shows that we are dealing here with a hybrid swarm, including tetraploids and various derivatives from them. But since the tetraploids have migrated beyond the limits of the parent subspecies, the recognition of this hybrid swarm as a distinct subspecies seems to be fully warranted.

The classical collections of J. Ball (in Herb. Berol.) were all made in the Grand Atlas Mts., except one from Mogador, on the coast in the westernmost province of Haha. Of these collections, the one from Ait Mesan, May 12–17, 1871, is accepted as the type (cf. fig. 276, *a-n*).

The hypothetical origin of subsp. *stellata* through hybridization between the two subspecies mentioned above is also in line with its extreme variability in habit, shape of leaves, and size of heads, florets, and achenes. Some of the more striking variants are described as m.v. 31–40. Some of these are apparently hybrids or derivatives from hybrids between subsp. *stellata* and subsp. *taraxacifolia* (cf. m.v. 38, 39). Probably hybridization between subsp. *stellata* and subsp. *myriocephala* will account for the long-leaved, small-headed plants with very small shortly beaked achenes collected by Ibrahim in 1881 at "Takreda" in "southeastern Ntifa," Morocco, cf. specimens (B, K, PC); the location of this district and place is not given in Stieler's or the Times Atlas, nor is it mentioned in Encyclopaedia Britannica, ed. 11.

The comparison of subsp. *stellata* with *C. foetida* L. var. *maritima* Boiss. by Thellung (Fl. Adven. Montpel. 581. 1912) was probably occasioned by his finding multiluted or repressed specimens of the former (cf. m.v. 31).

Morocco: Grand Atlas, Ait Mesan Valley, 1200–1400 m, *J. Ball* in 1871 (B, UCf) type; *ibid.*, Urika Valley, 960–1200 m, *J. Ball* in 1871 (B); *ibid.*, N. slope, near Tasseremont, 1000–1200 m, *J. Ball* in 1871 (B); *ibid.*, above Seksoua, 1200–1600 m, *J. Ball* in 1871 (B) m.v. 30; Casablanca Prov., Masagan, *Askenasy* in 1882 (G) m.v. 39; Haha Prov., hills near Mogador, *J. Ball* in 1871 (B, PC, UCf); Grand Atlas (southern), Keira, *Hooker* in 1871 (K); Ksima Prov., *Cosson* in 1874 (K); Anti-Atlas (S.W. Morocco), Kest Mts., near Taltemsem, 1700 m, *Maire* #01 (UC) m.v. 31;

S.W. Morocco, mountains, Ida Qubouzia, Takoust and Ait Zelten, *Cosson* in 1874 (K) m.v. 32; *ibid.*, *Cosson* in 1876 (B); Grand Atlas (western), Amismiz, south of Marrakesh, 1000–1100 m, *Maire* in 1925 (UC); Tagounit, *Ibrahim* in 1884 (B); Tell Atlas, Taferalt, *Faure* in 1930 (UC) m.v. 33; Tangier, *Pau* in 1921 (Bar) m.v. 40. Algeria: W. Oran, Tlemcen, around Terny, 1200 m, *Faure* in 1930 (UC); Oran, Santa-Cruz, *Faure* in 1936 (UC); Oran, Vidi-bel-Abbas, *Warion* in 1873 (G) m.v. 38; Oran, fields, *Balansa* 664 (K, DL, Ms) m.v. 41; Oran, between Mascara and Dublineau, *Babcock* 250 (UC); Oran-Alger, Dahra, clayey fields (spec. not seen) ex descr. Pomel, 1875, m.v. 36; E. Dahra reg., *Babcock* 266, 267 (UC) m.v. 37; Alger, between Tomba de la Chrétienne and Hamam Rijha, *Babcock* 263 (UC) m.v. 34; Alger, between Hamam Rijha and Marguerite, *Babcock* 264a (UC) m.v. 35.

Minor Variants of C. vesicaria stellata

31. (*C. taraxacifolia* var. *sulphurea* Maire et Wilczek, ex Maire, loc. cit.) Low, decumbent plants; caudical leaves up to 10 cm long, about 3 cm wide, finely pubescent; stem branched from base, branches up to 10 cm long, decumbent, few-headed; flower heads, bracts, achenes, and pappus typical, except the flower color, which is very pale yellow. Mutilated by grazing and probably repressed by environmental conditions. Chromosomes of progeny of *Maire* 201, $2n=16$. *J. Ball* in 1871 (B), calcareous rocks above Seksaoua, 1200–1600 m, Grand Atlas, Morocco; *Maire* 201 (UC), near Taltemsen, 1700 m, Kest Mts., Anti-Atlas, S.W. Morocco.

32. Stem and branches deep purple, inner achenes like those of subsp. *taraxacifolia*; plant 5 dm high, robust; caudical leaves 14 cm long, 4 cm wide, lateral segments salient, finely pubescent; stem remotely 3-branched, branches very strong, elongated, exceeding axis, few-headed, cymose-corymbiform; heads typical; style branches yellow; achenes bifurc; marginal achenes 5 mm long, beakless; inner achenes deep tawny, 6 mm long, abruptly attenuate into a fine beak equal to body; pappus 5 mm long. The deep purple stem and dark abruptly attenuate achenes suggest that this plant is a hybrid between subsp. *stellata* and subsp. *taraxacifolia*. *Cosson* in 1876 (K), Ida Qubouzia, Takoust and Ait Zelten, mountains, S.W. Morocco.

33. Heads smaller and achenes shorter than usual; plant 5 dm high, slender; caudical leaves up to 30 cm long, 3 cm wide, oblanceolate, dentate to lyrate-pinnately parted with very long terminal segment and few lateral segments, finely pubescent, petiole narrow, equal to blade; cauline leaves similar or sessile, stem remotely branched from below middle, lower branches short, aggregate inflorescence a few-headed compound cyme; involucre 9–10 mm high; florets 8–9 mm long; style branches green; achenes bifurc, 4.75–5.5 mm long; pappus 4–5 mm long. Chromosomes, $2n=16$, identical with those of my Oran plant (*Babcock* 250) which approaches the type of subsp. *stellata*. Apparently a derivative form with typical chromosomes but rather small heads, florets, and achenes, and the long-petioled leaves found in Hooker's plants from the Grand Atlas. The cultivated progeny had 16 chromosomes, and were more robust and constant in leaf shape and inflorescence. *Faure* in 1930 (UC), Taforalt, Tell Atlas, Morocco.

34. Stem tall, slender, branched above, branches spreading, terminated by a small, few-headed cyme; peduncles short, slender; involucre 8 mm long, 4 mm wide; involucre bracts, receptacle, and achenes like those of subsp. *myriocephala*. From this fragmentary specimen the hybrid nature of the plant is suggested only by the slender stem, peculiar habit, few-headed cymes, and somewhat larger heads. But in plants grown from seeds taken from this specimen the leaves are like those of subsp. *taraxacifolia* in both shape and size, whereas in habit and head characters these plants are uniform and closely resemble their parent. Also, two of these plants had $2n=8$ chromosomes. Thus, it appears that my original specimen (263) may represent a distinct true-breeding race with leaves like subsp. *taraxacifolia* and inflorescence and fruits like subsp. *myriocephala*. But whether this specimen was merely a sporadic individual produced by a fortuitous combination of chromosomes in an earlier hybrid between the two subspecies, or whether it represents a considerable population of the same intermediate type, is not known. Ex hort. genet. Calif. 31.2843–1, 2, 5, cult. from seeds taken from the following: *Babcock* 263 (UC), between Tomba de la Chrétienne and Hamam Rijha, Alger Prov., Algeria.

35. Only 1.5 dm high; root slender, woody; caudex 6 mm wide, marked with scars of old leaves; caudical leaves 9 cm long, up to 2 cm wide, lyrate-pinnatifid with retrorse lateral segments; stem slender, closely branched from near base upward, lower branches long, each branch with a small several-headed cyme at summit; involucre tomentose and densely gland-pubescent with short fine pale hairs; marginal achenes 3.5 mm long, similar to those of subsp. *myriocephala*, inner achenes 5 mm long, 0.5 mm wide, subterete, gradually attenuate into a beak $\frac{1}{2}$ as long as the whole achene; pappus 4 mm long. This diminutive, atypical plant was growing near plants (cf. m.v. 30) which proved to be an autotetraploid form of subsp. *myriocephala*; but, from the *taraxacifolia*-like leaves and coarser achenes, this specimen must be a product of hybridization between the two subspecies. *Babcock* 264a (UC), route Alger–Oran, between Hamam Rijha and Marguerite, Algeria.

36. (*C. hirsuta* Pomel, loc. cit.) Since no specimen has been seen by the present writer the original

description, translated in full from the French, is here given: "Heads in umbelliform corymbs at the extremity of the branches, forming a fastigiate corymb. Involucre with outer bracts lax, ovate, obtuse, concave, widely membranous, strongly hairy on outer face; inner bracts twice as long, subtomentose, hairy on outer face. Achenes rough, gradually attenuate with beak only $\frac{1}{4}$ longer than body. Lower leaves lyrate-pinnately parted with segments, lobes or teeth remote, terminal segment very large, attenuate into a narrow petiole; cauline leaves sessile, amplexicaul with lacinate auricles, middle ones pinnatifid, uppermost dentate or entire. Stem erect, branched, from a taproot, monocarpic. Plant hairy throughout, the hairs a little dusky. Flowering May. Clayey fields in Dahra." Since Dahra is a district in E. Oran and W. Algeria, it lies within the range of subsp. *stellata* (cf. m.v. 37).

37. Heads, florets, and fruits small. Robust plants up to 7 dm high; caudical leaves up to 18 cm long, 5 cm wide, oblanceolate, acute, lyrate-pinnately parted with very large terminal segment, lateral segments few, remote, triangular, acute, petiole long; lower cauline leaves similar or sessile, middle ones lanceolate, acuminate, amplexicaul-auriculate, \pm lacinate; stem stout, erect, branched from near base upward, branches long, strong, semierect, nearly naked, bearing 1-4 few-headed congested cymes; involucre 7-9 mm long, 3-4 mm wide; outer bracts $\frac{1}{2}$ as long as the inner, lanceolate, acute; inner bracts lanceolate, obtuse, carinate, tomentose, sometimes gland-pubescent or setulose; florets 8-10 mm long; style branches green; achenes pale brown, 4.5-6 mm long, all similar or marginal achenes gradually attenuate into a short coarse beak, ventrally flat or ridged, inner achenes subterete, fusiform, attenuate into a fine beak equal to body, 10-ribbed; pappus 3-4 mm long. Flowering May-June; flowers yellow, ligules purple on outer face. Chromosomes, $2n=8$. From the small heads, florets, fruits, and pappus these plants would appear to be forms derived from hybridization with subsp. *myriocephala*, the occurrence of dimorphic achenes in some of them strengthening this view. Hybridization between the two subspecies certainly occurs (cf. subsp. *myriocephala* and *stellata*) and is probably frequent. If the population here represented originated thus, the forms included here, as is shown by garden plants grown from the wild seed, have become relatively stable. That the large leaves and robust habit are not merely due to the partially shaded location is proved by the size of the plants and leaves of garden cultures grown in full sun, ex hort. genet. Calif. 31.2847-1, 2, 10, cult. from seed of no. 267. *Babcock 266a, b*, 267 (UC), among trees, near Hotel Ain n'sour, about 1150 m, E. Dahra reg., Algeria.

38. Achenes all beaked. Plant up to 4.8 dm high; caudical leaves up to 23 cm long, 6.5 cm wide, oblanceolate, acute, lyrate-pinnately parted with large terminal lobe and remote triangular or incised lateral segments, petiolate, finely pubescent or glabrescent; cauline leaves, lower similar or sessile, middle lanceolate, acuminate, runcinate, auriculate-amplexicaul; stem erect, branched from base upward, branches elongated, strict, stout, bearing few-headed congested cymes; peduncles short, rather stout; heads rather small; involucre 10 mm high, 4 mm wide; outer bracts few, linear, acute, tomentose or setulose; inner bracts about 10, lanceolate, obtuse, carinate, tomentose, finely gland-pubescent; florets 9-10 mm long; style branches green; achenes all similar, 6.5-7.5 mm long, subterete, fusiform, gradually attenuate into a fine beak shorter than body, 10-ribbed, ribs rather prominent; pappus 4-5 mm long, 1-seriate. Flowering April; flowers yellow, ligules purple on outer face. Intermediate between subsp. *stellata* and subsp. *taraxacifolia* and perhaps a variant derived from hybridization between the two. *Warion* in 1873 (G), Vidi-bel-Abbis, Oran, Algeria.

39. Similar to m.v. 38, except for longer caudical leaves; stem branched above middle; outer involucre bracts numerous, lanceolate, \pm imbricate, glabrescent; inner involucre bracts about 12, tomentulose; achenes lacking. This also may be a variant derived from subsp. *stellata* \times *taraxacifolia*. *Askenasy* in 1882 (G), Masagar, W. Morocco.

40. (*C. vesicaria* var. *tangerina* [Pau] Maire, ex Jahandiez et Maire, loc. cit.; *C. taraxacifolia* var. *tangerina* Pau, loc. cit.) Achenes all 4-4.5 mm long; marginal achenes obcompressed, not beaked, strongly ribbed; inner achenes strongly attenuate into a very short beak, ribbed and spiculate to the apex. Otherwise this plant is typical of subsp. *stellata*, although the heads are at the lower limit of size. Apparently it is a hybrid segregant in which the genes for the short achenes, from subsp. *myriocephala*, predominate, and the genes for the elongated beak have been lost or submerged in expression. *Pau* in 1921 (Bar), Tangier, Morocco.

41. Habit and leaves like those of m.v. 50 (p. 847). Heads rather small; involucre 9 mm high, 4-5 mm wide; outer bracts 5-7, lanceolate, acute, $\frac{1}{2}$ as long as the inner; inner bracts 7-10, lanceolate, carinate with median row of short black glandless setae; achenes 4.5-5.25 mm long, pale brown, marginal ones 0.7 mm wide, gradually attenuate into a very short beak, ventrally flattened, smooth, dorsally ribbed, inner ones 0.5-0.6 mm wide, subterete, fusiform, attenuate into a fine beak equal to body, 10-ribbed; pappus 4 mm long. Flowering March; flowers yellow, ligules purple on outer face. This plant is apparently a variant derived from hybridization with subsp. *myriocephala*. Only field studies can determine whether it represents an established constant population. *Balansa 664* Pl. d'Algerie, 1852 (K), uncultivated fields, Oran.

181, *e. Crepis vesicaria taraxacifolia* (Thuill.) Thell., ex Schinz et Keller, Krit. Fl. Schweiz, ed. 3, 361. 1914. Plant annual or biennial, monocarpic, 0.3–8 dm high; caudical leaves oblanceolate to spatulate, often, like the stem, reddish-purple near the base, 4–30 (mostly 10–20) cm long, 1–6 (mostly 2–4) cm wide; upper cauline leaves lanceolate, acute or acuminate, auriculate-amplexicaul, the uppermost linear or bractlike; branches 1–25-headed, heads usually in open corymbiform cymes; peduncles 1–13 cm long, slender, not changed in fruit; heads erect, medium to small, many-flowered; involucre cylindric-campanulate, 8–12 mm long, 3–7 mm wide in fruit; outer bracts 6–12, lanceolate or sometimes ovate-lanceolate, not imbricate, acute, sometimes pubescent or setulose, rarely setose; inner bracts 9–13, often shortly gland-pubescent, sometimes setulose, rarely setose, becoming carinate, spongy-thickened in fruit; receptacle densely ciliate, cilia white, 0.3–0.5 mm long; corolla (9) 11–12 mm long; ligule up to 1.75 mm wide, reddish-purple on outer face; teeth 0.1–0.15 mm long; corolla tube about 3.5 mm long, pubescent with acicular hairs 0.05–0.2 mm long; anther tube about 3.5 × 1 mm dis.; appendages 0.7 mm long, oblong, acute; filaments 0.5 mm longer; style branches 1.5–2 mm long, 0.1 mm wide, green or rarely yellow; achenes monomorphic, pale brown, (5) 6–8 (9) mm long, subterete, constricted at the narrow pale-calloused base, gradually attenuate into a fine beak equal to or slightly longer than the body, 10-ribbed, ribs narrow; pappus 4–6 mm long, 1–2-seriate. Flowering Feb.–Oct. Chromosomes, $2n = 8, 16$. See pl. 32 and figs. 277–279.

Crepis taraxacifolia Thuill., Fl. Par. 409. 1799.

C. polymorpha Pourr., Mem. Acad. Toul. 3: 317. 1788, non Wallr.

C. tectorum Vill., Dauph. 3: 144. 1789, non L.

C. umbellata Thuill., Fl. Par., ed. 2, 1799.

C. ruderalis Bouch., Fl. Abbev., ed. 3, 59. 1803.

C. praecox Balb., Mem. Acad. Sci. Turin 7: 353. 1803–1804.

C. taurinensis Willd., Sp. Pl. 3: 1595. 1804.

C. scabra Willd., Sp. Pl. 3: 1603, 1804.

C. cinerea Desf., Tabl., ed. 1, 89. 1804.

Barkhausia taraxacifolia DC., Fl. Fr., ed. 3, 4: 43. 1805.

C. vesicaria Balb., Fl. Taur. 93. 1806, non L.

C. rubicaulis Pers., Syn. Fench. Bot. 2: 375. 1807.

C. biennis Lapeyr., Abr. Pyr. 84. 1813.

C. intybacca Brot., Phyt. Lusit. 1: 57. t. 26. 1816.

C. recognita Hall. f., Naturw. Anzeig. 1: 90–91. 1818.

Barkhausia laciniata Lowe, Trans. Camb. Phil. Soc. 4: 25. 1833.

Barkhausia Haenseleri Boiss., ex DC., Prod. 7: 153. 1838.

Barkhausia heterocarpa Boiss., Voy. Bot. Esp. 742. 1839–1845.

C. Hensleri F. Schultz, Flora 23: 718. 1840.

C. laciniata F. Schultz, loc. cit.

C. numidica Pomel, Nouv. Mat. Fl. Atlan. 261. 1875 *fide* Batt. et Trab., Fl. Alg. 563. 1888–1890.

C. Hackelii Lange, Kjoeb. Vidensk. Meddel. 228. 1877–1878; Willk., Ill. Fl. Hisp. 1: 75. t. 51A. 1881–1885.

Hieraciodes taraxacifolium, O. Kuntze, Gen. 1: 346. 1891.

C. erythia Pau, Act. Soc. Esp. Hist. Nat., ser. 2, 24: 137. 1895 ex descr.

C. rutilans Lacaita, Jour. Linn. Soc. Bot. 44: 128. 1918.

W. Europe from the Adriatic to the North Sea, and throughout France, central to S. Spain and Portugal; S. England; N. Africa from E. Algeria to W. Morocco; Madeira, where it was probably introduced from Portugal by early explorers (it is widely distributed and common around Funchal); adventive in the Canary Is., E. and W. coasts of North America, New Zealand, and Australia. Fields, waste places and borders of woods from sea level to 1200 m, and in the Pyrenees to 2700 m. This subspecies, obviously, is adapted to cooler climates than is subsp. *typica*.

This subspecies is extremely polymorphic, including an extensive series of vari-

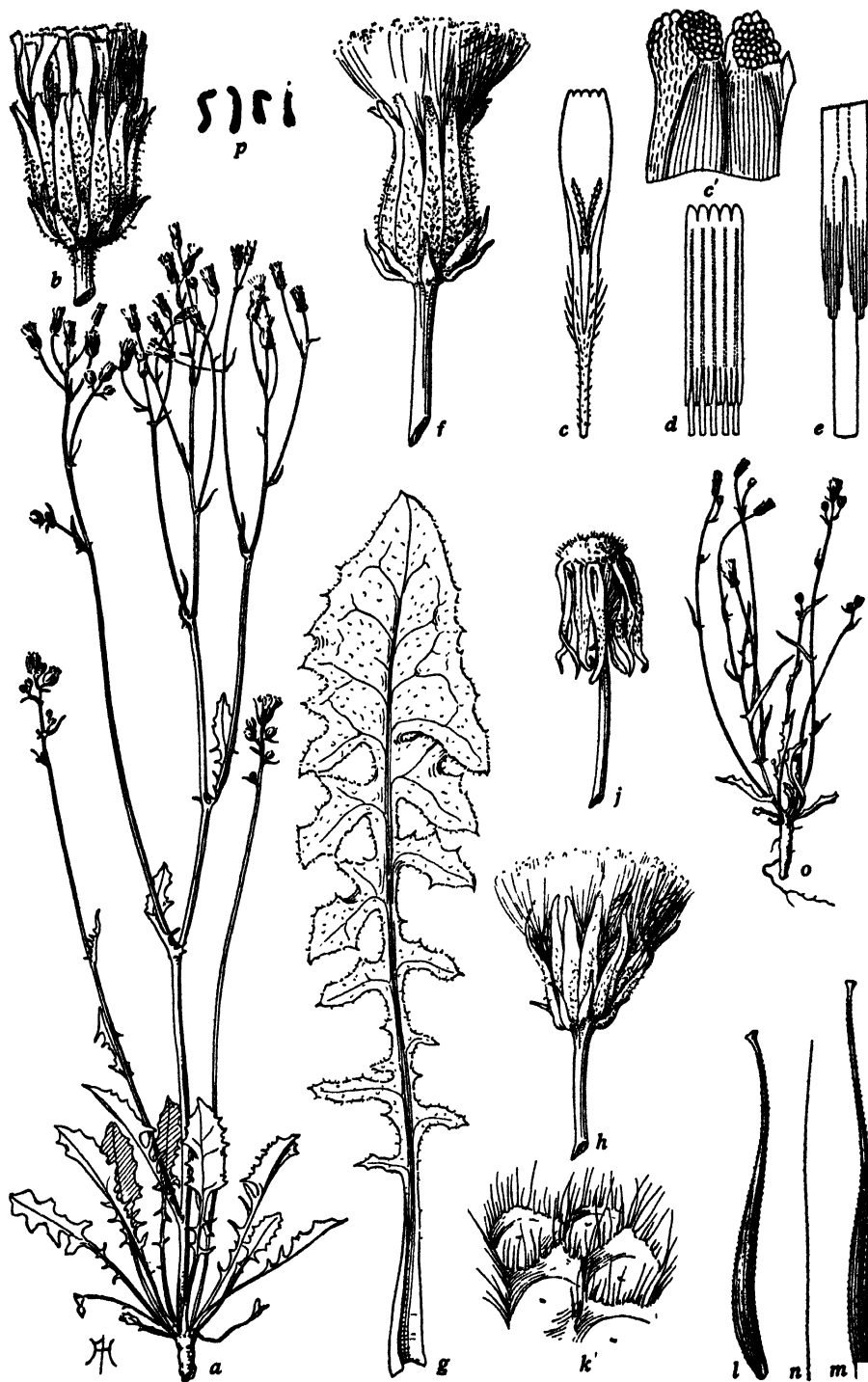


Fig. 277. *Crepis vesicaria taraxacifolia*, a-f, from Hall 12372 (UC 346456); g-n, from Hall 12461 (UC 346472); o, m.v. 43, from Hall 12487b (UC 346458); p, from hort. genet. Calif. 1064 (grown from seeds received from Zurich, Switzerland, through Dr. Carl Schröter): a, plant, $\times \frac{1}{4}$; b, flower head, $\times 2$; c, floret lacking ovary, $\times 4$; d, detail of ligule teeth, $\times 50$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, nearly mature head, $\times 2$; h, caudical leaf, $\times 1$; i, fruiting head, $\times 2$; j, old head, $\times 2$; k, detail of receptacle, $\times 20$; l-n, 2 achenes and a pappus seta, $\times 8$; o, plant, $\times \frac{1}{4}$ (the stems were more decumbent than is indicated here); p, somatic chromosomes, $n = 4$, $\times 1250$.

ants, none of which appears to be sufficiently distinct or constant to warrant its recognition as a subspecies, although several have been described as species. The peculiarities of many of these forms undoubtedly are due to genetic variations, and their inconstancy results from intercrossing and recombination of characters. At the same time, the wide diversity of environmental conditions under which this subspecies occurs must account for some of the most striking variants, such as the low spreading plants of sandy wastes and some of the robust plants found in moist rich soils. But certain forms of low stature, which occur locally in the warm region of E. Spain, are certainly tetraploids (cf. m.v. 64–66). Certain gigantic variants also are very probably tetraploids, although this has not been demonstrated cytologically. Furthermore, there are occasional forms which appear to be hybrids between this subspecies and subsp. *typica*, *myriocephala*, *stellata*, *andryaloides*, and *congenita*. On morphological grounds subsp. *taraxacifolia* also seems to be the closest relative of both subsp. *hyemalis* and subsp. *proleptica*. This might be taken to indicate that subsp. *taraxacifolia* is the present-day representative of the ancestral stock from which the whole inclusive species has evolved. Comparative morphology, however, indicates that subsp. *proleptica* and *congenita* are the most primitive types in this assemblage. But subsp. *taraxacifolia* is the most “aggressive” or “successful” of all eight subspecies, and this is the chief reason why it has invaded the areas of most of the others. It is very probable that any two of the eight subspecies would hybridize naturally if given the opportunity. Some of the subsp. *taraxacifolia* hybrids and other variants which seem mostly likely to cause difficulty in classification are discussed under m.v. 42–68.

Italy: Turin, *Huguenin*, Rehb. Fl. Germ. exs. 440 (K, G, Po); between Ventimiglia and La Mortola, *Hall 12115* (UC); Verona dist., *Rigo* in 1900 (UC) near m.v. 46 but not setose; Mt. Baldo, *Rigo* in 1902 (B). **Greece:** Corfu, near Monrepos, *Druce* in 1914 (Oxford-Druce), as *C. rutilans* = m.v. 46. **Switzerland:** *Thomas*, Rehb. Fl. Germ. exs. 594 (K); Vaud, Bex, *Schleicher* (Po). **Germany:** Ulm, *Hegelmeyer* (UC); Munich, *Grabmayr* (K). **England:** Kent, Rochester, *Stevens* (K); Middlesex, Wembley, *Milne-Redhead 268* (K); Wilts, Potterne, *Turrill Z144, 149* (K); Surrey, Norbury, *Raine* in 1905 (G) m.v. 42; Wrenham, *Drinkwater* in 1908 (K) m.v. 42. **France:** Somme *Copeneau* in 1898 (Po); Vosges, *Raine* in 1906 (G); Hautes-Alpes, Gap, *Faure* in 1900 (UC); near Dijon, *Hall 12427a, b* (UC) *b* = m.v. 43; Pont du Gard, *Hall 12461* (UC); Toulon, Cap Brun, *Huet* in 1870 (Bur) m.v. 44; Bouches du Rhone, St. Julien, *Roux* in 1867, Fl. exs. Billot 3877 (K) m.v. 43; *ibid.*, near Martigues, *Roux* in 1868 (G) m.v. 43; near Marseille ? ex herb. J. Gay (K) m.v. 43; Pont du Gard, *Hall 12490, 12463* (UC) m.v. 43; Aude, La Nouvelle, *Sennen* in 1903 (UC) m.v. 43; Pont du Gard, *Hall 12485* (UC) m.v. 44; *ibid.*, *Hall 12461* (UC) m.v. 45; E. Pyrenees, Cerdagne, *Sennen* in 1917 (Bar) m.v. 47; Hautes Pyrenees, Gedre, *Bodere* in 1883 (BML). **Spain:** Catalonia, near Barcelona, *Bourgeau 43* (K); Catalonia, Montserrat, Vallfogona de Rincorb, *Font Quer* in 1917 (Bar); Catalonia, Manresa, *Font Quer* in 1912 (Bar) m.v. 43; Barcelona, near Sarria, in 1868 (Bar) m.v. 43; Zaragoza Prov., near Calatayud, *Vicioso* in 1911 (BML) m.v. 65; *ibid.*, *Vicioso* in 1912 (Bar) m.v. 65; central Spain, near Madrid, *Jeronimo* in 1918 (K); Salamanca, *Lacaita 95/23* (BML); Estremadura, Sierra de Guadalupe, near Mirabel, *Lacaita* in 1923 (BML); Valencia, Gandia, *Lacaita* in 1884 (BML) m.v. 48; Teruel, *Benedicto* in 1895, 1896 (Bar); Albacete Prov., Almansa, *Font Quer* in 1919 (Bar) m.v. 66; Albacete, Calar del Mundo, *Cuatrecasas* in 1923 (Bar) close to m.v. 63; Jaen, Cerro del Buitre, 1200 m, *Cuatrecasas* in 1925 (Bar); Jaen, Carboneras, 1300 m, *Cuatrecasas* in 1925 (Bar); Jaen, Venta del Vidrio, *Cuatrecasas* in 1925 (Bar); Jaen, Vertiente del Ponce Lucia el Peru, *Cuatrecasas* in 1925 (Bar) m.v. 61, as *C. taraxacifolia* fa. *splendens*; Jaen, El Boqueton, *Cuatrecasas* in 1925 (Bar) m.v. 62, as *C. taraxacifolia* fa. *splendens*; Alicante Prov. (?), Mt. Montgo (Mongo ?), *Gros* in 1923 (Bar) m.v. 63, as *C. taraxacifolia* fa. *ad C. Haensleri* verg.; Alicante, Hifac, slopes of the promontory, *Ellman and Sandwith 1192* (K) m.v. 48; Alicante Prov., Denia, rocks of the Mongo, *Ellman and Sandwith 1130* (K, UC) m.v. 67; Alicante Prov., near Orihuela, *Hackel* in 1876 (C) as *C. Hackelli* Lange = m.v. 64; Sierra Callosa, near Orihuela, *Winkler* in 1876 (Mo) m.v. 64; Sierra Callosa, near Orihuela, *Ellman and Sandwith 453* (UC) m.v. 64; Malaga, Guadalhorce B., *Winkler* in 1876 (G); Malaga, *Boissier* in 1838 (DL) m.v. 49; Cadiz, Vejer, *Willkomm 564, 566* (K, B); Andalusia, Sierra Morena, *Lacaita 305/25* (BML) m.v. 68; Cadiz, Vejer, *Willkomm 569* (K, B) m.v. 50. **Portugal:** without locality, *Brotero* in 1808 (DC Prod. vii: 154

n. 11) m.v. 51; Lisbon, fields, *Welwitsch it. Lusit.* 283 (K, B) m.v. 51; Coimbra, *Moller*, F. Schultz herb. norm. n.s. 12: 1147 (G) m.v. 51; Elvas, near Badajoz, *Babcock 240a, b, c* (UC) c = m.v. 51. **Madreia:** along Cuniso road, *Lowe* in 1829 (K) m.v. 52; *Lemann* in 1825 (K) m.v. 52; Boroaca, *Mandon 151* (K, B, P) m.v. 52; Funchal, *Bornmüller 878, 878b* (Genoa, UWG, P, PA) m.v. 52, 53; *ibid* (?) *Lowe* (DC) m.v. 52, 53; Pta. da Cruz, *Lowe* in 1860, 1867 (K) m.v. 53; Gonzales, *Babcock 200, 207, 208, 209, 210, 211* (UC) m.v. 52, 53; Curral das Freidas, *Babcock 235, 237* (UC) m.v. 52, 53; N. coast, near Entroza, *Babcock 226a* (UC) m.v. 54. **Algeria:** Oran, Gambetta, *Babcock 256* (UC) m.v. 43; S. Oran, St. Maur, *Pailloux* in 1830 (DS); Alger, Miliana, *Pomel* in 1859 (Alger, UC) perhaps a product of hybridization between this subspecies and subsp. *typica*; Grand Kabylie, near Yakouren, *Babcock 257* (UC) m.v. 55; Philippeville, *Choulette* in 1858 (B); near Bossuet, *Faure* in 1930 (UC) m.v. 56. **Morocco:** near Tangier, Cap Spartel, *J. Ball* in 1871 (B); Taforault, near Berkane, *Faure* in 1930 (UC); Camp Boulhaut, rocky fissures, *Maire* in 1925 (UC) m.v. 58.

Minor Variants of C. vesicaria tarazacifolia

42. (*C. tarazacifolia* var. *gigantea* [Rouy] Thell., *loc. cit.*, sub *Barkhausia* Rouy, Fl. Fr. 9: 213. 1905.) Very robust; caudical leaves up to 30 cm long, 7 cm wide or wider; stem 7–14 dm high; heads, florets, and achenes probably larger than typical of the subspecies. Some plants of this form may be merely ecads; but it is probable that cases of tetraploidy are involved. These forms, however, are not to be confused with such amphidiploids as subsp. *stellata*. *Drinkwater* in 1908 (K), Wrenham, England; *Raine* in 1905 (G), Norbury, Surrey, England.

43. (*C. recognita* Hall. f., *loc. cit.*; *C. polymorpha* Pourr., *loc. cit.*; *C. numidica* Pomel p.p., *fade Batt. et Trab.*, *loc. cit.*; *C. vesicaria* var. *recognita* [Hall. f.] *Maire*, ex *Jahandiez et Maire*, Cat. Pl. Maroc. 3: 851–852. 1934.) Stems several, divaricate, ± decumbent; cauline leaves reduced, mostly bractlike; peduncles often elongated, very slender; heads, florets, and achenes often ± reduced. Suppression due to various causes, such as poor soil and competition with other species, may be sometimes responsible for this striking modification in habit. This is indicated by the fact that the whole plant is sometimes depauperate. It is probable, however, that one or more ecotypes are involved, or, at least, that there is a genetic basis for this variant. This is strongly indicated by the occurrence of plants of this type among garden cultures grown from seed collected in an area where this variant is of frequent occurrence. The plant from Oran (*Babcock 256*) may represent an introduction from S. France. *Roux* in 1867 (K, Bur), St. Julien, Bouches du Rhone, France; *J. Gay* ? (K), near Marseille, France; *Hall 12463, 12490* (UC), Pont du Gard, France; *Hall 12437b* (UC) near Dijon, France; *Sennen* in 1903 (Ms, UC), La Nouvelle, Aude, France; *Font Quer* in 1912 (Bar), Manresa, Catalonia, Spain; *Brandt 22* (B), Algeciras, Spain; *Babcock 256* (UC), Gambetta, a suburb of Oran, Algeria.

44. Resembles m.v. 43, but depauperate, very slender, simulating *C. bellidifolia*. Plant 0.5–1.3 dm high; caudical leaves up to 6 cm long, 1.5 cm wide, oblanceolate, lyrate-pinnately parted, lateral segments narrow, remote; cauline leaves mostly bractlike; stems 2–3, decumbent, 2–4 headed; peduncles up to 9 cm long, very slender; heads small; involucre 9 mm high, 3–4 mm wide; outer bracts 7–9, conspicuous, longest nearly $\frac{1}{2}$ as long as the inner, ovate-lanceolate, acuminate, becoming lax; inner bracts 10–15; corolla 12 mm long; anther tube 2.5 mm long; style branches green; achenes 7 mm long, beak equal to body; pappus 4.5 mm long, 1-seriate. Flowering June; flowers yellow with purple on outer face of ligules. In addition to three plants of this variant, there are in the first collection cited below two plants without flowers or fruits in which the caudical leaves are pectinately pinnatifid with very narrow terminal segment and narrow remote acute lateral segments. Presumably they are the subspecies and they may represent merely a leaf variation of this form. *Hall 12485* (UC), stony ridge in zone of *Quercus ilex*, Pont du Gard, France; *Huet* in 1870 (Bur), Cap Brun, Toulon, France.

45. Habit atypical, with 4 stoutish semidecumbent stems. Plant 5.3 dm high; caudical leaves up to 16 cm long, 2.5 cm wide, oblanceolate, pinnately parted with narrow denticulate terminal and lateral segments and long narrowly winged petiole; stems branched from the middle, branches stout, erect; peduncles short, congested near summit; involucre and receptacle typical; florets numerous, 9–10 mm long; style branches green; achenes 5–6 mm long, beak 1.5–2.5 mm long, fine; pappus 4.5 mm long, 1-seriate. Flowering June; flowers yellow, purple on outer face of ligules. *Hall 12461* (UC), partly shaded, sandy mound, Pont du Gard, France.

46. (*C. rutilans* Lacaita, *loc. cit.*) Plant hispid with purple setae except leaf blades, which are pubescent on both sides with short pale hairs; caudical leaves up to 27 cm long, 3.5 cm wide, retosely dentate or lyrate-pinnately parted, terminal segment large, hastate, lateral segments few, small, remote, petiole long, narrow; stem erect, stout, branched near summit; heads erect, medium; outer bracts lanceolate, not imbricate, brown-scarious, like inner bracts gland-pubescent and setose near apex, the setae purple; florets 8 mm long, yellow, reddish-purple on outer face of ligules; achenes 5–6.5 mm long, abruptly attenuate into a slender beak longer than the body;

marginal achenes mostly similar to inner ones but sometimes gradually attenuate into a coarse beak; pappus 3.5 mm long. Flowering April. This plant may be a derivative from hybridization with subsp. *typica*. *J. Ball* in 1877 (K), near seashore, Corcyra (= Corfu); *Bicknell* in 1889 (B), Parc de Monrepos, Corfu; *Druce* in 1914 (Oxford-Druce), near Monrepos, Corfu, Greece.

47. (*C. ceratana* Sennen, in litt.; *Barkhausia ceratanica* Sennen in Herb. Bar.) Low, diffuse, strongly rooted. Plant biennial, 1.5 dm high; caudical leaves (first season) oblanceolate, obtuse, denticulate, shortly petiolate, later ones (on flowering plant) pinnate with close acute segments, densely pubescent; caudex swollen; cauline leaves similar or sessile, lanceolate, acuminate, lacinate near base; stems 3, densely branched from near base, branches numerous, short, few-headed; peduncles 0.5–6 cm long; involucre 9 mm long, 4 mm wide; outer bracts lanceolate, scarious-margined; florets 11 mm long; anther tube 3 mm long; style branches green; achenes pale brown, gradually attenuate into a beak shorter than the body; pappus 4–5 mm long, 1-seriate. Flowering Sept.; flowers yellow, purple on ligules. In addition to specimens cited below, flower heads were received from Frère Sennen with notation, "E. Pyrenees, 1200–2700 m." *Sennen* in 1917 (Bar), fields at Cailloste, 1400 m, Cerdagne (= La Cerdana ?) E. Pyrenees, France.

48. (*C. Haensleri* [Boiss.] F. Schultz, loc. cit.) Leaves glabrescent, often nearly entire. The type (DC) is mostly destroyed by insects, but fragments agree fairly well with the description. The following description is based on specimens cited below: Plants 1.8–4 dm high; caudical leaves up to 12 cm long, 3 cm wide, oblanceolate to elliptic, denticulate, dentate or runcinate, glabrescent; cauline leaves mostly small, sessile, subamplexicaul; stem erect, branched above, or stems 2–6, branched from near base or above; petioles short, forming a close corymbiform cyme; involucre up to 10 mm long; outer bracts lanceolate, $\frac{1}{3}$ – $\frac{1}{2}$ as long as the inner, becoming scarious, lax; style branches green; achenes 5–7 mm long, beak equal to or shorter than body; pappus 4–5 mm long. *Boissier* in 1838 (DC), d'Alhausin, Granada; *Ellman and Sandwith* 1192 (K), slopes of promontory, Ififac, Alicante; *Lacaita* in 1884 (BML), Huerta, Gandia, Valencia; *Fritze* in 1873 p.p. (B), Sierra de Sujas, Malaga, Spain.

49. Lower cauline leaves 2–3 cm long, oblanceolate, lyrate, petiolate, auriculate-amplexicaul, sparsely hispidulous; stem divaricately branched, branches long, strict, each branch bearing a congested cyme of about 8 small, many-flowered heads; involucre 7 mm long, 4 mm wide, campanulate; outer bracts linear, $\frac{1}{4}$ as long as the inner; inner bracts 15, lanceolate, acute, tomentose, setose, the setae short, blunt, black, becoming carinate, ultimately reflexed, appressed pubescent on inner face; receptacle densely ciliate, cilia white; anther tube about 3.5×1 mm dis.; achenes 4–5 mm long, fusiform, subterete, marginal ones enclosed in bracts, laterally compressed, very shortly and coarsely beaked, inner ones with beak nearly equal to body, yellowish-brown near base, purplish-brown above, beak dull purple, 10-ribbed, ribs narrow; pappus white, 3.5 mm long, 1-seriate, caducous. This plant, known only from the fragments of one specimen, may be a distinct species, as is indicated by the short linear outer involucral bracts, the shortly beaked compressed marginal achenes, and the uniquely colored inner achenes. Yet it may be merely an extreme variant of subsp. *taraxacifolia*. *Boissier* in 1838 (DL), fields near Malaga, Spain.

50. Approaches m.v. 51; cauline leaves subamplexicaul; involucre very dark colored, 8–10 mm long, 5–6 mm wide; outer bracts lanceolate, acuminate, longest $\frac{1}{2}$ as long as inner bracts; inner bracts tomentose, gland-setulose with fine black setules; florets 10–12 mm long; style branches green; achenes 5–6 mm long, gradually attenuate into a beak shorter than the body, 10-ribbed, ribs rather prominent; pappus 4–5 mm long, 2-seriate. *Willkomm* 569 (K, B), Vejer, Cadiz, Spain.

51. (*C. intybacca* Brot., loc. cit.) Cauline leaves oblanceolate to lanceolate, nearly entire or denticulate, cordate-amplexicaul, auriculate. Caudical leaves oblanceolate, acute, petiolate, denticulate to runcinate-pinnatifid; stem stout, erect, tall, branched above; peduncles short, forming rather small congested cymes; involucre 10 mm long, 4 mm wide; outer bracts lanceolate, acuminate, obtuse at apex; inner bracts lanceolate, obtuse; corolla 11–12 mm long; ligule 1.5 mm wide; corolla tube 3.5 mm long; anther tube 3.75×1 mm dis.; appendages 0.7 mm long; filaments 0.6 mm longer; style branches 1.75 mm long, green; achenes 6 mm long, gradually attenuate into a beak shorter than the body, 10-ribbed; pappus 4–5 mm long, 2-seriate. Flowering Apr.–May; flowers yellow, ligules purple on outer face. Chromosomes, $2n = 8$. (Pl. 32, a. Fig. 278.) *Brotero* in 1808 (DC), Portugal; *Welwitsch iter Lusit.* 283 (K), fields near Lisbon, Portugal; *Moller herb. norm. F. Schultz* 1147 (B, G), Coimbra, Portugal; *Babcock* 240c (UC), Elvas, E. Portugal.

52. (*Borkhausia laciniata* var. *pinnatifida* Lowe, loc. cit.) Leaves glabrous, glabrescent or sparsely pubescent. Robust single-stemmed plants up to 9 dm high, or low, single stemmed, few-headed, or, like m.v. 43, many-headed; caudical leaves up to 23 cm long, 4 cm wide, oblanceolate, lyrate-pinnatifid or runcinate-dentate, petiolate; lower cauline leaves similar or sessile, middle cauline leaves lanceolate, acuminate, \pm lacinate; stem paniculately branched from near base or middle upward, branches long, branched near summit, 2–11-headed; heads small to medium, many-flowered; involucre 8–12 mm long, 4–6 mm wide; outer bracts lanceolate, acuminate; inner

bracts lanceolate, obtuse; corolla 11–13 mm long; style branches green; achenes pale to dark brown, 7–9 mm long, gradually attenuate into a beak equal to body, 10-ribbed, ribs rather prominent; pappus 4–5 mm long, 1–2-seriate. Flowering Mar.–May; flowers yellow, ligules purple on outer face. Chromosomes, $2n=8$. (Pl. 32, b, c.) In addition to this variant and the next, there are numerous intergrades in Madeira exhibiting varying degrees of laciniation of the cauline

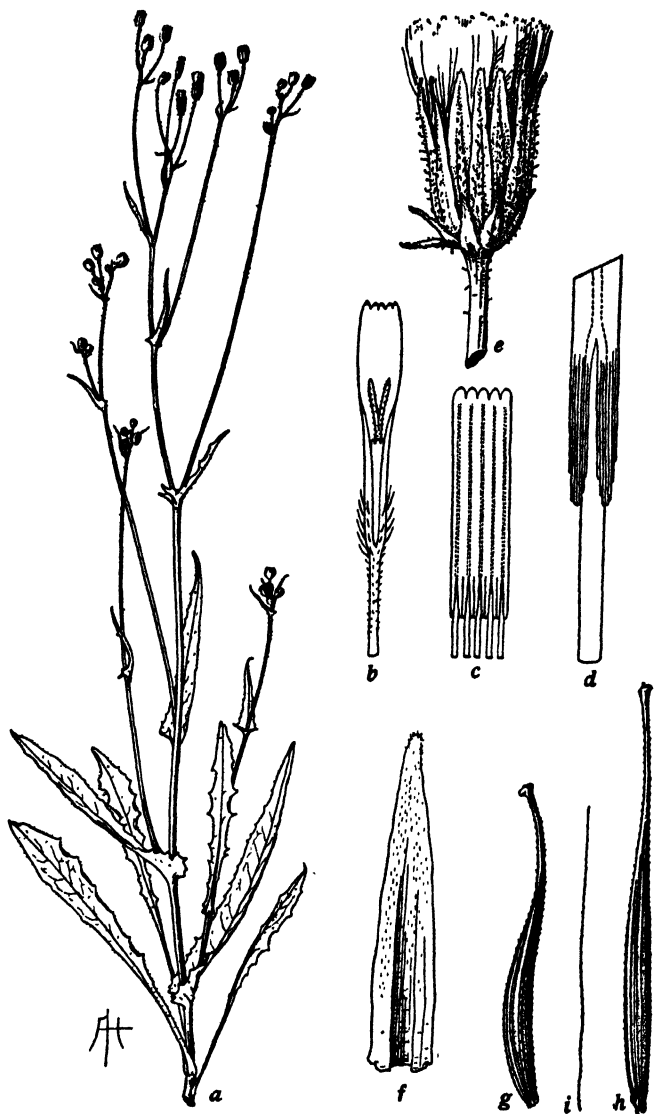


Fig. 278. *Crepis vesicaria taraxacifolia*, m.v. 51, from Babcock 240c (UC 429521; compared with *C. intybacea* Brot.): a, plant, $\times \frac{1}{4}$; b, floret lacking ovary, $\times 4$; c, anther tube, $\times 8$; d, detail of appendages, $\times 32$; e, fruiting head, $\times 2$; f, inner involucre bract, inner face, $\times 4$; g–i, 2 achenes and a pappus seta, $\times 8$.

leaves and dissection of the caudical leaves, the two characters on which Lowe's varieties are primarily based. See also m.v. 54. Lowe (DC, P, K) without definite locality; Lemann in 1825 (K); Mandon 151 (K, B, P), Boroaca; Bornmüller 878 (UWG, P, Genoa, P.A.), Funchal; Babcock 200, 207, 209 (UC), near Funchal; Babcock 235, 236 (UC), Curral dos Freidas, 750 m, trail from Boa Ventura to Funchal, Madeira.

53. (*Borkhausia laciniata* var. *integrifolia* Lowe, loc. cit.) Leaves glabrous or glabrescent, often

dark green. Robust or slender single-stemmed plants, 2–8 dm high; caudical leaves up to 33 cm long, 5 cm wide, oblanceolate, almost entire, finely denticulate or runcinate, petiolate; lower cauline leaves similar or sessile, middle ones lanceolate, acuminate, entire or denticulate, amplexicaul-auriculate; stem paniculately branched from near base or middle upward, branches long, cymosely branched near summit, 2–7-headed; heads small to medium, many-flowered; involucre 9–11 mm long, 4–6 mm wide, the bracts like those in m.v. 52; corolla 11–13 mm long; style branches green; achenes pale to dark brown, 7–9 mm long, gradually attenuate into a beak equal to or shorter than the body, 10-ribbed; pappus 4–5 mm long, 1–2-seriate. Flowering Mar.–May; flowers yellow, ligules purple on outer face. Chromosomes, $2n = 8$. (Pl. 32, d.) Extreme examples of this form stood out strikingly from m.v. 52 when the two were seen side by side in a dry ravine near Gonzales, south of Funchal, the dark green, glabrous, nearly entire leaves of the plants of this variant being conspicuous. But seeds collected from wild plants did not reproduce the form constantly, and various combinations of leaf color and leaf shape occur. Hence, Lowe's two varieties appear to be outstanding but inconstant variants from a mixed population. The general similarity of the Madeiran forms to m.v. 51 strongly indicates that the Madeiran population arose from plants introduced from Portugal. Such introduction probably occurred after the Portuguese colonization; and it may have occurred as early as the fifteenth century, this subspecies being widely distributed on the S. side of the island and being especially common around Funchal. However, one of Lowe's several specimens, which were given the number 190 (K), was collected on Deserta Grande I., where, acc. to Lowe (552), it occurs. Although it seems improbable, the possibility nevertheless exists that during the earlier history of the subspecies in Madeira there was hybridization between it and some native species, such as subsp. *andryaloides* or *C. divaricata*. This improbability holds for the following reasons: (1) the introduction undoubtedly occurred at Funchal and there is nothing to indicate that either of the native species existed in that district; (2) the native species differ in so many characters from subsp. *taraxacifolia* that much more diversity in the present population of the latter would be expected had such hybridization occurred (cf. m.v. 54). It is much more likely that the original introduction from Portugal consisted of m.v. 51 and some other form or forms more nearly typical of subsp. *taraxacifolia*, and that these have continued to interbreed. At the same time, new gene mutations affecting leaf color, pubescence, etc., have probably occurred and have been preserved under the influence of the Madeiran environment. In this connection it is of interest to note that at a later time Lowe (612) was inclined to refer his *B. laciniata* to *C. intybacea* Brot. (= m.v. 51). Lowe (DC, K) without definite locality; Bornmüller 778b (PA), near Funchal; Babcock 208, 210, 211 (UC), near Gonzales, east of Funchal; Babcock 237 (UC), Curral dos Freidas, trail from Boa Ventura to Funchal, Madeira.

54. Intermediate variants, exhibiting various combinations of the two subspecies, occur along the N. coast of Madeira from the Ribeiro do Inferno to Boa Ventura. Those more nearly resembling subsp. *andryaloides* are mentioned under that species. The present group verges more toward subsp. *taraxacifolia* in habit, leaf shape, and flower color, although in most of them the peduncles and involucre have the black setae so characteristic of subsp. *andryaloides*, and in some of them, as in the latter, the flower color is pale yellow. From my collection of m.v. 52 and 53 in the central uplands of the island, along the trail from Funchal to Boa Ventura, it appears that subsp. *taraxacifolia* was brought across the island from Funchal to the N. coast, where it met subsp. *andryaloides*. Babcock 224, 225, 226, 228, 231 (UC), vineyards, trails, and seacliffs, N. coast, Madeira.

55. Resembles m.v. 43, except stems rather strict. Leaves narrow, pinnately parted with narrow terminal and lateral lobes; cauline leaves similar or sessile; stem erect, 4-branched from base, 3 branched above base, branches long, erect, 6–16-headed; heads small; involucre 8 mm long, 4 mm wide; outer bracts lanceolate, acute, $\frac{1}{2}$ as long as inner bracts, fully scarious with dark brown median stripe, lax; inner bracts lanceolate, obtuse, carinate, tomentose, gland-pubescent or setulose near apex; florets 7–8 mm long; style branches green; achenes brownish-yellow, slender, 4.5–6 mm long, subterete, fusiform, attenuate into a fine beak longer than or equal to body, 10-ribbed; pappus 3–3.5 mm long, 1 seriate. Flowering May; flowers yellow, ligules purple on outer face. Chromosomes, $2n = 8$. From the small heads, florets, and achenes this plant would seem to be a form derived from hybridization with subsp. *myriocephala*, but its seed reproduced the type quite faithfully in the garden. Hence, if it is of hybrid origin, it is a stable derivative. It may be merely a genetically distinct race of subsp. *taraxacifolia*. Ex hort. genet. Calif. 31.2838–6 (UC), grown from seed of the next; Babcock 257 (UC), exposed hillside, about 300 m, near Yakouren, Grande Kabylie, E. Algeria.

56. Similar to m.v. 43 in habit; densely gland-pubescent throughout. Caudex 1 cm wide; divided above into several stems; stems divaricate, procumbent, branched from the base upward, branches elongated, 1–2-headed; lowest cauline leaves oblanceolate, acute, runcinate-pinnatifid, petiolate, middle cauline leaves lanceolate, acute, auriculate-amplexicaul; heads long, narrow, many-flowered; involucre up to 12 mm long, 5 mm wide; outer bracts few, $\frac{1}{4}$ as long as the inner; inner

bracts 10–14, lanceolate, obtuse; florets 11 mm long; style branches pale yellowish green; achenes 7–8 mm long, gradually attenuate into a beak shorter than the body, 10-ribbed; pappus 5 mm long, 1-seriate. Flowering June; flowers yellow, ligules purple on outer face. This anomalous plant differs from both subsp. *taraxacifolia* and subsp. *stellata*, but may well be a hybrid derivative. *Faure* in 1930 (UC), rocky meadow, 1000 m, between Bossuet and Ain-Tindamine, Algeria.

57. (*C. erythia* Pau, *loc. cit.*) A translation of Pau's description is as follows: "My plants, probably inferior individuals, are about 15 cm high; the caudical leaves being in some plants longer than the inflorescence, which consists of a corymb of a few flowers; the bracts are linear-lanceolate, entire; exterior bracts appressed or slightly lax, interior ones ciliate at the lanceolate acute apex. . . . A species intermediate between *C. vesicaria* and *C. taraxacifolia* Thuill.; but closer to the latter and above all to its variety *C. recognita* Hall. f." (Spec. not seen by me. The name *C. erythia* Pau has been wrongly applied by Font Quer in *herb.* to *C. Fontana*, q.v.) Acc. to Pau, Puerta de Santa Maria and Puerto Real, Cadiz, Spain.

58. Cauline leaves, as in m.v. 51, auriculate-amplexicaul, and the mature achenes rather broad and shortly beaked, marginal achenes laterally compressed. Caudical leaves up to 8 mm long, 1 mm wide, lyrate-pinnatifid with remote small triangular lateral segments and very narrow rachis and petiole; cauline leaves few, small, linear; stems arcuate, about 4 dm high, remotely 3-branched above middle, branches strict, 3–5-headed; peduncles short; heads small, erect, many-flowered; involucre 8–9 mm long, 5 mm wide, the outer and inner bracts typical; corolla 10 mm long; ligule 1.25 mm wide; corolla tube 2–3 mm long; anther tube 3.75×1 mm dis.; appendages 0.75 mm long; filaments short; style branches 1.75 mm long, dark green; mature marginal achenes 5 mm long, 0.4–0.5 mm wide, broadest near base, gradually attenuate into a rather coarse beak about 1 mm long, 10-ribbed, ribs rather strong; inner achenes not seen, probably longer and longer beaked; pappus 4 mm long. Flowering Apr.; flowers yellow, ligules red on outer face. *Maire* in 1925 (UC), fissures of quartzite rocks, Camp Boulhaut, Morocco.

59. Very robust, caudical leaves broad, lower branches stout, elongated, achenes rather broad and strongly ribbed. Caudical leaves up to 21 cm long, 7 cm wide, obovate to oblanceolate, acute, lyrate-pinnately parted; lower cauline leaves similar, sessile, amplexicaul, lacinate near base; lower stem and branches purplish; involucre 8–10 mm long, 6–7 mm wide; corolla 11 mm long; ligules purplish on outer face; anthers 3 mm long; achenes 6–7.5 mm long, 0.5–0.6 mm wide, beak 2–3 mm long, ribs rather prominent; pappus 4.5 mm long. Apparently a robust, broad-leaved shade form with rather coarse achenes. The pollen is regular, 3-pored, and averages about 28μ in diameter. *Font Quer* in 1923 (Bar), in shade, 300 m, Montgo, Regno Val. (= Mongo, between Denia and Javea, Alicante Prov.), Spain.

60. A hybrid of subsp. *taraxacifolia* \times *congenita*, from gross morphology of the plant. Root vertical, 6 mm wide, woody; caudex 8 mm wide, bearing scars of old leaves below, leafy above; caudical leaves up to 25 cm long, 5.5 cm wide, oblanceolate, acute, lyrate-runcinate-pinnatifid, attenuate into a narrowly winged petiole $\frac{1}{4}$ as long as whole leaf; lower cauline leaves dentate, the petiole broadly winged, subamplexicaul; middle and upper cauline leaves lance-linear, acuminate, denticulate or entire; stem 5.8 dm high, erect, robust, purple near base, remotely branched from base upward, lower branches long, strictly erect, cymose at summit, with more numerous heads than in subsp. *congenita*; peduncles short, strong, arcuate; heads erect, smaller than in subsp. *congenita*; involucre 9 mm long, 5–6 mm wide, yellowish tomentulose, \pm setulose, the setae black; outer bracts 5–6, nearly $\frac{1}{2}$ as long as the inner, lanceolate, acute, becoming scarious and lax; inner bracts 12; florets 10 mm long; ligules yellow, purplish on outer face; style branches green; achenes yellowish-brown, 6 mm long, 0.4 mm wide, attenuate into a slender beak $\frac{1}{3}$ – $\frac{1}{2}$ as long as whole achene; pappus 5 mm long, 2-seriate. The purple stem, pinnatifid leaves, green style branches, smaller heads, more slender achenes, and 2-seriate pappus are reminiscent of subsp. *taraxacifolia*, which occurs in this region. But the robust plant, very large caudical leaves, peculiar cauline leaves, paniculate habit, very long strict branches, and pale brown color of the achenes indicate the influence of subsp. *congenita*. *Benedicto* (Bar), as *C. taraxacifolia* var. *heterocarpa* Willk., Monreal del Campo, Teruel Prov., Spain.

61. Stature, habit, and leaves more like those of subsp. *congenita*. Involucres rather dark colored, gland-setulose, setules short, dark; outer bracts narrow, lanceolate, $\frac{1}{4}$ as long as the inner; receptacle ciliate, cilia white; style branches green; achenes finely beaked, as in subsp. *taraxacifolia*. This combination of characters strongly indicates a hybrid origin. Probably this is an amphidiploid derivative from subsp. *congenita* \times *taraxacifolia*. *Cuatrecasas* in 1925 (Bar, as *C. taraxacifolia* fa. *splendens*), Vertiente del Ponce Lucia el Peru, 1300 m, Sierra Magina, Jaen, Spain.

62. Habit, leaves, especially the cauline leaves, and inflorescence more like those of subsp. *congenita*. Stem and lower branches deep reddish-purple, as in subsp. *taraxacifolia*; caudical leaves elliptic to oblanceolate, shortly petioled; heads rather small, the involucre 9–10 mm long; style branches green. The pollen grains are 3-pored but irregular, ranging from 28 to 34μ , and

averaging about 33μ in diameter. Supposedly another amphidiploid derivative. *Cuatrecasas* in 1925 (Bar, as *C. taraxacifolia* fa. *splendens*), in shade of rocks, N. crags of El Boqueton, 1300 m, Sierra Magina, Jaen, Spain.

63. Corolla 13–15 mm long; anther tube 4.5 mm long; achenes coarsely beaked; and pappus dusky white. Plant 3–4 dm high; involucre gland-setulose, setules black; outer involucre bracts

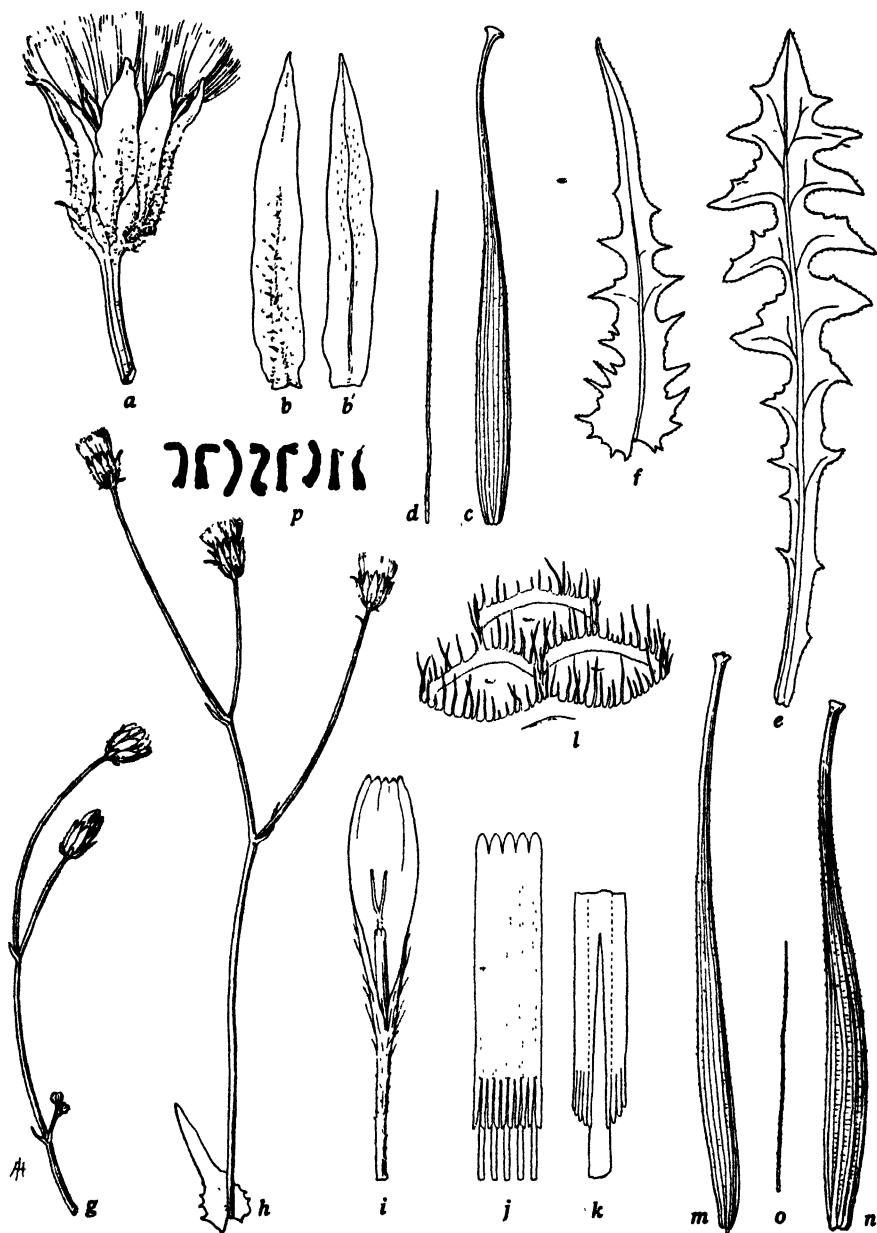


Fig. 279. *Crepis vesicaria taraxacifolia*, m.v. 64, a–d, from isotype of *C. Hackelii* Lange (C); e–p, from hort. genet. Calif. 27.1873–3 (grown from seed collected at type locality of *C. Hackelii*, Sandwith 453, UC 499380): a, head, $\times 2$; b, b', inner involucre bract, inner and outer faces, $\times 4$; c, d, achene and pappus seta, $\times 8$; e, caudical leaf, $\times \frac{1}{2}$; f, cauline leaf, $\times \frac{1}{2}$; g, flowering branch, $\times \frac{1}{2}$; h, fruiting branch, $\times \frac{1}{2}$; i, floret lacking ovary, $\times 4$; j, anther tube, $\times 8$; k, detail of appendages, $\times 32$; l, detail of receptacle, $\times 25$; m–o, achenes and pappus seta, $\times 8$; p, somatic chromosomes, $2n = 16$ ($x = 4$), $\times 1250$.

lanceolate or linear, $\frac{1}{3}$ as long as inner bracts in fruiting heads; style branches light green; achenes pale brown, 7–8 mm long; pappus 4.5 mm long. Although verging toward subsp. *taraxacifolia* in involueral characters and the green style branches, these plants show some influence of subsp. *congenita*; and they, too, are probably amphidiploid derivatives. The pollen is very irregular, ranging from 26 to 38μ , averaging 30μ in diameter, and some 4-pored grains are present. Gros in 1923 (Bar, as *C. taraxacifolia* var. *Haensleri*), among trees, 900 m, Mt. Montgo, "Regno Val." (= Mongo, between Denia and Javea, Alicante Prov.), Spain.

64. (*C. hackelii* Lange, loc. cit.) Plants perennial, 1–2 dm high, divaricately branched from the base, few-headed; leaves densely pubescent with pale glandless setules; style branches yellow; achenes stramineous, 6–8.5 mm long, 0.5–0.7 mm wide, gradually attenuate into a definite beak shorter than the body, 10-ribbed, ribs rather strong; pappus 4 mm long; receptacular cilia short, fine, white. Chromosomes, $2n = 16$. (Fig. 279.) Willkomm (216) lists this plant as a xerophyte occurring on calcareous rocks in Orihuela, Spain. That this is a tetraploid form of subsp. *taraxacifolia*, which has been repressed by environmental conditions, is shown by the fact that plants grown at Berkeley from seeds taken from Ellman and Sandwith's plant no. 453 were over 3.5 dm high and bore leaves with the normal pubescence of subsp. *taraxacifolia* and achenes 8–11 mm long. These achenes were also more typical of subsp. *taraxacifolia*, both in respect to color and relative proportions of body and beak, than those borne by the wild parent plants. This tetraploid form, being so repressed by environmental conditions as to be mistaken for a distinct species, is not without interest. In view of this evidence it seems probable that the following two variants (65, 66) are also tetraploids. This is also indicated by comparison of pollen grain sizes. In the wild plant (in Herb. UC), Ellman and Sandwith 453, the pollen was fairly regular and averaged about 28μ in diameter, and that of one of its cultivated descendants averaged about 29μ , whereas in a cultivated plant of a strain of subsp. *taraxacifolia*, known to have $2n = 8$ chromosomes, the pollen averaged about 26μ in diameter. Hackel on Mar. 24, 1876 (C, isotype), on rocks near Orihuela, Alicante Prov., Spain; Winkler on Mar. 25, 1876 (Mo), Sierra Callosa, near Orihuela; ex hort. genet. Calif. 27.1873–3, cult. from the following ($2n = 16$): Ellman and Sandwith 453 (UC), rocky slopes of Sierra Callosa, above Callosa, near Orihuela, Alicante Prov., Spain.

65. Plants perennial, 0.7–2.7 dm high; root strong, woody; caudex 1–2 cm wide; stem erect, robust, branched above or from the base, lower branches elongated, few-headed; leaves densely and finely pubescent with yellow glandless hairs; style branches yellow or sometimes green; achenes about 8 mm long, gradually attenuate into a beak shorter than the body, rather strongly ribbed; pappus 4–5 mm long. Pollen grains on one plant averaged 30μ in diameter, as compared with 26μ for a plant of a strain known to have $2n = 8$ chromosomes. This is apparently another tetraploid form somewhat resembling the preceding, but more robust. Vicioso on June 21, 1911 (BML), waste places and along roads, Calatayud; Vicioso on April 30, 1912 (Bar), fields, waysides, and waste places, Calatayud, Zaragoza Prov., Spain.

66. Plants perennial, 2–2.5 dm high; root slender, woody; caudex 1 cm wide; leaves densely pubescent with yellow glandless hairs; stem erect, slender, branched above or from base, lower branches elongated, few-headed; involucre 9–13 mm long; style branches yellow; achenes 9–11 mm long, gradually attenuate into a beak shorter than the body, finely ribbed; pappus 5–6 mm long. Pollen grains on one plant averaged 29μ in diameter as compared with 26μ for a plant known to be of a strain with $2n = 8$ chromosomes. This is apparently another tetraploid, intermediate between the two preceding in size. Font Quer in 1919 (Bar), Almansa, Albacete Prov., Spain.

67. A hybrid of subsp. *taraxacifolia* \times *congenita*. Caudical leaves up to 20 cm long, 6 cm wide, runcinate-pinnatifid with broad triangular lateral lobes; stem robust, branched above or from the base, lower branches elongated, many-headed; involucre 9–10 mm long; outer bracts very short and narrow; style branches green; achenes brownish-yellow, 7 mm long, 0.5–0.7 mm wide, gradually attenuate into a beak shorter than the body, ribs rather strong, extending to apex; pappus 4–5 mm long; receptacular trichomes coarse, yellow, shining. This combination of characters suggests a hybrid between subsp. *taraxacifolia* and *congenita*; and this inference is supported by the fact that segregation of various characters occurred among the garden progeny of the wild plants collected by Ellman and Sandwith. For example, among the three cultivated specimens cited below, one has coarse yellow trichomes on the receptacle, another has coarse white trichomes, and the third has fine short white trichomes or "cilia." In three of the cultivated offspring the chromosome number was $2n = 16$, which would indicate that these are amphidiploid derivatives. Ex hort. genet. Calif. 32.2777–5, 6, 7 (UC), cult. from seeds taken from the following: Ellman and Sandwith 1130 (K, UC), rocks of the Mongo, Denia, Alicante Prov., Spain.

68. Achenes brownish-yellow, 7–9 mm long, gradually attenuate into a beak shorter than the body, 10-ribbed, the ribs rather strong, extending to the apex; pappus 4.5–5 mm long; style branches yellow or green. Otherwise typical. The *congenita*-like achenes and the yellow style

branches on one of the two plants cited below suggest that these are the products of hybridization between subsp. *taraxacifolia* and *congenita*. Although the plants are fairly robust, the pollen grains average only 26–27 μ in diameter. Hence, these appear to be diploid derivatives, and amphidiploidy may not have been involved in their ancestry. *Lacaita* 305/25 (BML), among rocks, Depeñaperros pass, Sierra Morena, W. Andalusia, Spain.

181, f. *Crepis vesicaria andryaloides* (Lowe) Bab., Univ. Calif. Publ. Agr. Sci. 6: 369. 1939. Plant perennial or biennial, sometimes flowering the first year, 1.3–7 dm high; caudex woody, 4–7 mm wide; caudical leaves oblanceolate, acute or obtuse, dentate to lyrate-pinnately parted, pubescent especially on lower face or sometimes glabrous, midrib prominent, whitish or reddish; upper cauline leaves lanceolate, nearly entire, auriculate-amplexicaul, uppermost sometimes black-setose; lower branches elongated, arcuate, 3–10-headed in corymbiform cymes, like upper stem and peduncles conspicuously black-setose, sometimes canescent-tomentose at the bifurcations; peduncles 1–6 cm long, not changed at maturity; heads erect, medium, about 60-flowered; involucre cylindric-campanulate, 10–12 mm long, 4–5 mm wide in fruit; outer bracts about 8, about $\frac{1}{3}$ as long as the inner, lanceolate or linear, dark green or black, glabrous, tomentose or \pm black-setose; inner bracts 12–15, with a median dorsal row of black glandless or glandular setae, these sometimes long and spreading, becoming dorsally carinate and spongy-thickened; receptacle ciliate, cilia short, white; corolla 13–15 mm long; ligule about 2 mm wide, pale yellow without red on outer face; teeth 0.3–0.9 mm long; corolla tube 3–4 mm long, pubescent with stout acicular hairs up to 0.5 mm long; anther tube (3)4 \times 1 mm dis.; appendages about 0.7 mm long, lanceolate, acute; filaments 0.5–1 mm longer; style branches 2–3 mm long, 0.15 mm wide, dark green; achenes uniform, dark brown, 5–9 (mostly 7–8) mm long, about 0.6 mm wide, the beak shorter than the body, 10-ribbed, ribs narrow, yellow-calloused at the hollow base; pappus yellowish-white, 4–5 mm long, 2-seriate. Flowering May–July. Chromosomes, $2n = 8$. See pl. 33 and figs. 280–282.

Crepis andryaloides Lowe, Trans. Camb. Phil. Soc. 4: 25. 1831; Fl. Mad. 1: 559. 1868.

Borkhausia hieracioides Lowe, Trans. Camb. Phil. Soc. 4: 27. 1831; Fl. Mad. 1: 556. 1868.

Borkhausia dubia Lowe, Trans. Camb. Phil. Soc. 4: 27. 1831.

Borkhausia comata Lowe, loc. cit.

C. comata Banks et Solander, ex Lowe, Fl. Mad. 1: 556. 1868.

Borkhausia hieracioides et *dubia* (Lowe) DC., Prod. 7: 157. 1838.

C. hieracioides et *dubia* (Lowe) F. Schultz, Flora 23: 718. 1840.

C. auriculata Sol., ex Lowe, Fl. Mad. 1: 556. 1868.

Hieracioides Loweianum O. Kuntze, Gen. 1: 345. 1891.

Madeira, in the N. central highlands and at lower altitudes on cliffs and near openings of ravines along the N. edge of the island from Ribeiro do Inferno to Entroza and perhaps farther east and west. Acc. to Lowe (556), about the middle of the nineteenth century his variety, *nigricans*, which he considered "the usual mountain and probably normal form of the species," was found in most of the ravines in the N. part of the island above 600 m alt.; therefore, at that time, this was the most widespread *Crepis* species on the island. But in 1930 the writer was unable to find a single *Crepis* plant around and below the Boca dos Torrinhas, one of the higher localities particularly mentioned by Lowe. It is possible that eventually this subspecies will be exterminated by the goats that graze the highlands and by the peasants who cut it for fodder in certain localities where, as I was told by natives in 1930, it is still abundant. This seems to be the almost certain fate of *C. divaricata*, which is restricted to a single promontory where goats are pastured. But subsp. *andryaloides* is still so widely distributed that it will probably persist for many years.

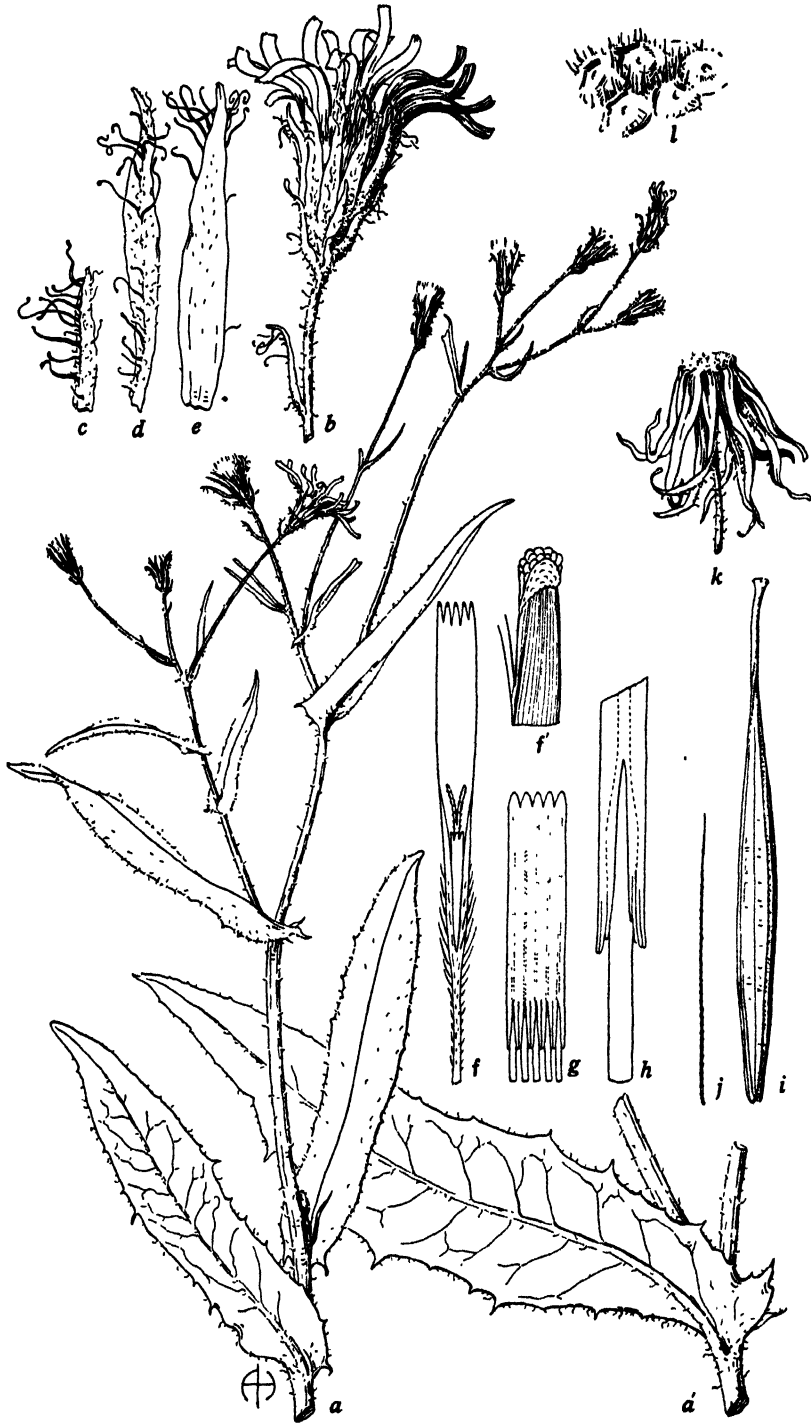


Fig. 280. *Crepis vesicaria andryaloides*, a-j, from type = m.v. 69 (DC); k, l, from Lowe in 1851 (K): a, 1 branch, $\times \frac{1}{2}$; b, head, $\times 2$; c-e, 1 outer and 2 inner involucral bracts, $\times 4$; f, floret lacking ovary, $\times 4$; f', detail of ligule tooth, $\times 25$; g, anther tube, $\times 8$; h, detail of appendages, $\times 32$; i, j, achene and pappus seta, $\times 8$; k, old head, $\times 2$; l, detail of receptacle, $\times 16$.

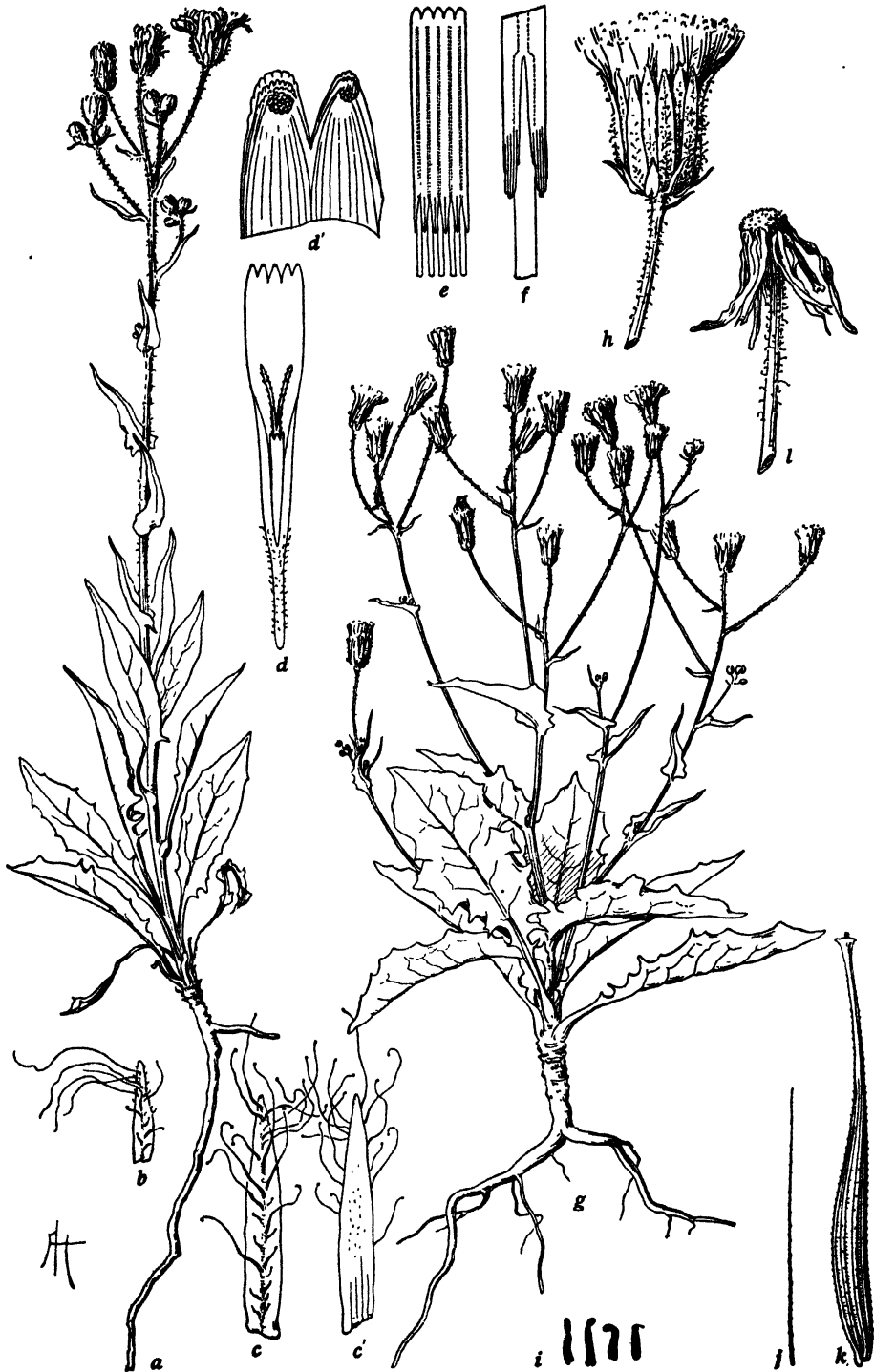


Fig. 281. *Crepis vesicaria andryaloides*, a-f, from Babcock 229b (UC 429527); g-l, from Babcock 221 (UC 429531): a, plant, $\times \frac{1}{2}$; b, outer involucral bract, $\times 4$; c, c', inner bract, outer and inner faces, $\times 4$; d, floret lacking ovary, $\times 4$; d', detail of ligule teeth, $\times 25$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, plant, $\times \frac{1}{2}$; h, fruiting head, $\times 2$; i, somatic chromosomes, $n = 4$, $\times 1250$; j, k, achene and pappus seta, $\times 8$; l, old head showing receptacle, $\times 2$.

At the same time, there is another biotic factor which may have a great influence on the ultimate fate of subsp. *andryaloides*. As a result of the introduction of subsp. *taraxacifolia* into Madeira hundreds of years ago, the latter subspecies has migrated (or has been carried) from the south to the north side of the island where it has hybridized with subsp. *andryaloides* and produced many intergrading, partly fertile forms (cf. m.v. 53, 77). This creates the possibility that subsp. *andryaloides* and *taraxacifolia* will gradually become merged into a population of intermediate forms on the north side of the island, whereas subsp. *taraxacifolia* may maintain itself as such indefinitely on the south side where it is most abundant. At any rate, the fact that subsp. *andryaloides* is producing vigorous, fertile hybrids with subsp. *taraxacifolia*, with a resulting hybrid swarm, is sufficient reason for the treatment of the former as a subspecies of *C. vesicaria*. Furthermore, subsp. *andryaloides* is closer to subsp. *taraxacifolia* morphologically than to *C. divaricata*.

The specimens collected by the author in 1930 have been compared with authentic specimens of Lowe, including the type. Although most of my specimens are smaller in stature than the type, yet in other respects they are essentially the same. Furthermore, they display the same variability in degree of pubescence as was observed by Lowe; and among them are included the two forms distinguished by him mainly from the appearance of the flower heads. In his var. *nigricans*, which appears to be the most representative form, he describes the florets as "somewhat more close and numerous with the ligules less produced," whereas in var. *laevigata* (cf. m.v. 76) he has this to say: "florets few, lax with elongated pendulous ligules." Although herbarium specimens and garden cultures exhibit these differences in appearance of the flowering heads, yet comparative measurements of marginal florets from the two forms fail to reveal much difference in length of the florets. The variation in appearance of the flower heads is probably due to some peculiarity in behavior of the florets during anthesis. Some variability in degree of yellow color in the ligules has also been noted, and these occur, as would be expected, in various combinations with varying degrees of pubescence and differences in other characters.

Considering the subspecies as a whole, there is marked variation in the achenes, especially in their length and in length of beak or degree of attenuativeness. The most extreme variations in the achenes have been found in the numbered variants described below. But the most striking variants of all are found in m.v. 71 and in intermediate forms between it and the type of the subspecies. In pl. 33 are reproduced photographs of the type of m.v. 71 (*C. comata* [Lowe] Banks et Sol.); m.v. 72, an intergrade closely resembling m.v. 71 in heads, florets, and achenes; and m.v. 70, one of Lowe's specimens of *C. dubia* which resembles m.v. 72 in habit but has glabrous involucre. See also figs. 280-282. Considering all the evidence, it seems most probable that m.v. 71 (*C. comata* [Lowe] Banks et Sol.) is a polyploid of some sort, perhaps an autotetraploid. Various intermediate forms might easily appear among the progeny resulting from intercrossing with diploids. Excepting the hybrids with subsp. *taraxacifolia*, which seem from their restricted distribution to be of recent origin, it appears that all the variations within this highly variable subspecies are the results of either genetic changes within the subspecies itself or the effects of radical environmental differences. In other words, subsp. *andryaloides* appears to have been completely isolated from *C. divaricata*, the only other *Crepis* species known to be indigenous on the island; and its contact with subsp. *taraxacifolia* appears to have been comparatively recent. But some of its present variability may be due to earlier hybridization with subsp. *taraxacifolia* or with *C. divaricata*.

Madeira: N. coast, high up the Rib. S. Jorge (cf. Lowe, Fl. Mad. 1: 559, 1868) Lowe in 1829 (DC, UCf) type = m.v. 69; near San Vicente, Lowe in 1837 (K, UCf), as *B. hieracioides* Lowe;

without definite locality, *Lemann* in 1837 (Bo); Boa Ventura, *Lowe* in 1846 (K) as *B. dubia* *Lowe* = m.v. 70; head of Rib. de João Delgada, *Lowe* in 1850 (Fl, UCf, G) m.v. 70; Torrinhãs or summit of Tombo Grande, *Lowe* in 1846 (P) m.v. 70; without locality, *Lowe* (BM) as *B. comata* *Lowe* = m.v. 71; Pico do Arieiro, among shrubs in rocky places, 1500 m, *Mandon* in 1865 (Bo, UCf) m.v. 71; without definite locality, *Mason* 97 (Bo, UCf) m.v. 72; without definite locality, *Mason* 216 (Bo) m.v. 73; without definite locality, *Mason* (Bo) m.v. 74; Entroza, seacliffs, *Lowe* in 1848 (G) m.v. 75; N. coast, along footpath from San Vicente to Ponta Delgada at Passo d'Areia, *Babcock* 222a, b (UC) m.v. 76; N. coast, along path on high cliff east of Entroza, about 333 m, *Babcock* 229a, b (UC) b = m.v. 76; N. coast, seacliffs between San Vicente and mouth of Ribeiro do Inferno, *Babcock* 220 (UC); N. coast, mouth of Ribeiro do Inferno, *Babcock* 221 (UC); N. coast, east of Passo d'Areia, *Babcock* 223a, b (UC) b = m.v. 77; seacliff road from S. Vicente to Seixal, east of Rib. do Inferno, *Lowe* in 1862 (US).

Minor Variants of C. vesicaria andryaloides

69. (*C. andryaloides* *Lowe*, Man. Fl. Mad. 1: 559. 1868.) Distinguished by *Lowe* from the type of his *B. hieracioides*, but almost solely, by its dark green leaves, which are gland-pubescent especially on the upper surface. The single specimen, cited below, was lifted in rosette stage and grown in *Lowe's* garden alongside a plant of typical *B. hieracioides*. The type specimen, in herb. DC., and *Lowe's* description were from this cultivated plant (his description has been supplemented by my own observations on the type specimen): 6–9 dm high; stem simple, erect, paniculately branched above middle; leaves dark green, pubescent with short gland hairs; caudical leaves up to 12 cm long, 2.5 cm wide, oblong, acute, finely denticulate; cauline leaves oblong, acuminate, denticulate, sessile, cordate-amplexicaul, acutely auriculate; aggregate inflorescence cymose-corymbiform; peduncles gland-hairy; involucre in anthesis 2.5–3 cm wide, gland-hairy with long black setae; outer bracts 6, linear, $\frac{1}{2}$ as long as the inner; corolla 15 mm long; ligule 1.25 mm wide; corolla tube 4 mm long, densely pubescent; anther tube 4×1 mm dis.; appendages 0.75 mm long, narrow, acuminate; style branches 1.3 mm long, green; achenes 8 mm long; gradually attenuate into a beak about 1.5 mm long; pappus 4.5 mm long. (Fig. 280.) *Lowe* in 1829–1830 (DC, UCf), cult. from a root collected high up Rib. de San Jorge, Madeira.

70. (*C. dubia* [*Lowe*] F. Schultz, loc. cit.; cf. pl. 33, c.) Plants 1.8–4 dm or taller; caudical leaves narrowly oblanceolate, acute or acuminate, denticulate, glabrous; cauline leaves lance-linear, acuminate, with rounded denticulate or minutely auriculate subamplexicaul base; stem branched from base upward; branches long, arcuate or strict, 1-headed or few-branched, 2–6-headed; heads erect, medium, many-flowered; involucre 10–12 mm high; bracts typical except black setae few or absent; corolla 13 mm long; ligule 2 mm wide; anther tube 4 mm long; style branches dark green; achenes 5.5–7 mm long, strongly attenuate upward, scarcely beaked, ribs and base as in typical forms; pappus typical. Absence of a definite beak on the achenes is a very unusual variation, except in species where it is the general rule to have unbeaked marginal achenes. In other respects, however, these plants closely resemble the type of subsp. *andryaloides*. Flowering June–July. *Lowe* in 1846 (K), Boa Ventura; *Lowe* in 1850 (Fl, UCf, G), rock at head of Rib. de João Delgada, Madeira.

71. (*C. comata* [*Lowe*] Banks et Sol., ex *Lowe*, Trans. Camb. Phil. Soc. 4: 27. 1833; *Crepis hieracioides* var. *crinita* *Lowe*, Man. Fl. Mad. 1: 556. 1868; cf. pl. 33, d, fig. 282.) Perennial, with thick fleshy rootstock; caudical leaves up to 14 cm long, 1.5 cm wide, oblong, acute, with broadly winged petiole and clasping base, irregularly pinnate, lateral segments oblanceolate, lanceolate or triangular, glabrous; lower cauline leaves similar except base broadly auriculate-amplexicaul, uppermost linear, entire and densely hirsute with long greenish-brown hairs; stems numerous, stout, divaricate-arcuate, 2.5 dm high, sulcate, hispidulous, branched near extremity; branches few but aggregate inflorescence broad, many-headed; heads erect, large, many-flowered; involucre broadly campanulate, up to 1 cm wide at base when mature, densely hirsute with long and short brown glandless or glandular hairs and, like peduncle, fuscous-tomentose at base; outer bracts 6–8, unequal, 6–10 mm long, lanceolate, acute, gland-hairy, apically tufted with long slender brown or greenish hairs, ventrally glabrous; inner bracts 10–13, about 15 mm long, lanceolate, obtuse, dorsally hirsute like outer bracts, ventrally pubescent toward tip; corolla 14 mm long; ligule 1.3 mm wide; ligule teeth 0.5–0.75 mm long; anther tube 4.3×1.25 mm dis.; appendages 0.75 mm long, obtuse; style branches 0.75 mm long, brown in sic.; achenes pale brown, 7–9 mm long, slender, terete, fusiform, very gradually attenuate into a beak 1–2 mm long, narrowed slightly to the small calloused base, about 12-ribbed, ribs narrow; pappus 4–5 mm long, 2-seriate. Flowering May–June; flowers pale yellow. The type specimen (BM) bears no data other than the following: "*Bark. comata* *Lowe*, *Crepis comata* MSS." Since it is in very poor condition, the above description is based on the specimen cited below, which is almost exactly like the type. *Mandon* 150 (Bo, UCf), Pico do Arieiro, among shrubs in rocky places, 1500 m, Madeira.

In the Manual, *Lowe* reduces *C. comata* to a variety of *C. hieracioides*, substituting the name,

orinita. In this connection he says in part: "The discovery of numerous intermediate forms necessitates the fusion even of Solander's plant (*C. auriculata* Sol.) together with my own two former species (*C. comata* and *C. dubia*) into one, though the shaggy bearded involucreal scales and peduncles of extreme forms, such as the original type of *C. comata* in BH. (= BM) give that variety a most distinct and peculiar aspect. It passes however gradually back through β (= var. *nigricans*),

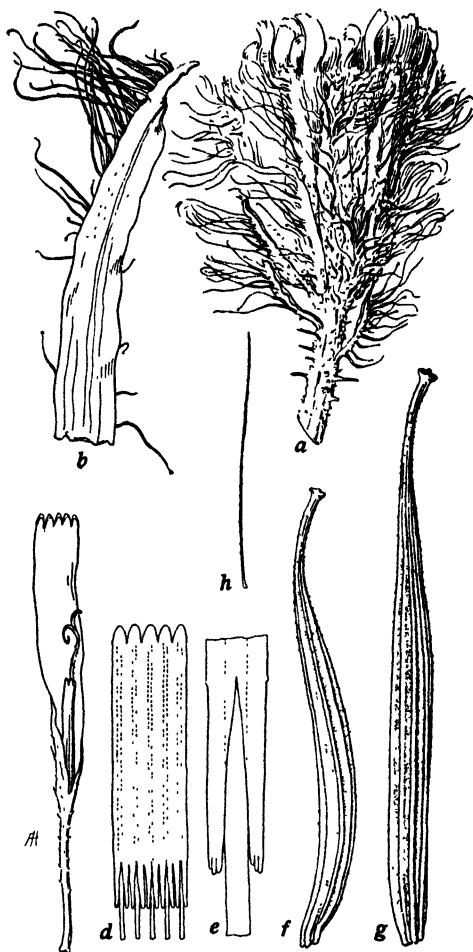


Fig. 282. *Crepis vesicaria andryaloides*, m.v. 71, from Mandon 150 (Bo, as *C. comata* [Lowe] Banks et Sol.; *C. hieracioides* var. *orinita* Lowe): a, head, $\times 2$; b, inner involucreal bract, $\times 4$; c, floret lacking ovary, $\times 4$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f-h, achenes and pappus seta, $\times 8$.

branched from near base upwards; branches long, arcuate, branched at extremity with 2-5 heads; peduncles short; heads medium, many-flowered; involucre 10-12 mm high, canescent-tomentose; outer bracts 10, about $\frac{1}{2}$ as long as the inner, with median dorsal black setae, becoming scarious; inner bracts 12, lanceolate, obtuse, with median dorsal black setae; ligules light yellow; style branches green; mature achenes lacking; pappus 5 mm long. Other hybrid forms, exhibiting more characteristics of subsp. *tarazacifolia*, were found in the same district. Babcock 223b (UC), N. coast, in grass near road east of Passo d'Areia, Madeira.

181, g. *Crepis vesicaria proleptica* subsp. nov. Herba perennis vel biennis 5-7 dm alta; caudex ligneus 0.5-1.5 cm latus; folia caudicalia circa 30 cm longa 5 cm lata

which seems to be the normal form of the species, into the comparatively denuded state, (= var. *laevigata*, cf. m.v. 76); the main distinctive features of all three in common being the peculiar light shining apple-green foliage, the mostly low habit, branched from base, the (tomentum) of peduncles and involucre, the peculiar black setules, the pale yellow flowers. The leaves vary from undivided to runcinate-pinnatifid in each of the three forms." The intermediate forms mentioned by Lowe are represented by m.v. 72-75.

72. Closely similar to m.v. 71 in heads, florets, and achenes, but it also resembles m.v. 70 in habit and leaf shape (cf. pl. 33, b). Mason 97 (Bo), no definite locality, Madeira.

73. Robust, as in m.v. 71, gland-hispid on upper stem and less hairy on upper leaves and heads; achenes 6-7 mm long, dark brown. Mason 216 (Bo), no definite locality, Madeira.

74. Resembles m.v. 71 in the hirsute involucre and uppermost leaves; plant tall (probably 6 dm high) and slender; cauline leaves resembling those of m.v. 71. Mason (Bo), no definite locality, Madeira.

75. Branches more strictly erect; cauline leaves acuminate auriculate; heads up to 5 mm wide at base; involucre bracts sparsely pubescent; achenes dark brown. Lowe in 1848 (G), seacliffs, Entroza, Madeira.

76. (*C. hieracioides* var. *laevigata* Lowe, loc. cit.) Plants 2-2.5 dm high; caudical leaves lanceolate, acute or acuminate, narrowly petiolate with broad clasping base; stem branched from middle or near base upwards; branches short, 1-3-headed; involucre 10 mm high; ligules pale lemon yellow, somewhat lax, making the flower heads appear somewhat larger than in the typical form; achenes and pappus typical. (Fig. 281, a-f.) Babcock 222a (UC), N. coast, along path from Sao Vicente to Ponta Delgada at Passo d'Areia; Babcock 229b (UC), N. coast, cliff east of Entroza, about 333 m, Madeira.

77. A hybrid of subsp. *andryaloides* \times *tarazacifolia*. Plant 2.5 dm high; caudical leaves oblanceolate, pinnately parted with narrow acute lateral segments; cauline leaves linear with broad lacinate auriculate-amplexicaul base; stem

oblanceolata dentata vel lyrato-pinnatifida; folia caulina similia vel sessilia amplexicaulia; caulis erectus 8–10-ramosus, ramis inferis elongatis ad summitatem cymose ramosis; pedunculi 3–11 cm longi stricti vel arcuati hispidulosi; capitula 50–60-flora; involucria 11–13 mm longa 6–8 mm lata nigro-virida setulosa; squamae exteriores 6–8 lanceolatae, interiores 12–16 lanceolatae ad maturitatem carinatae et spongioso-incrassatae; receptaculum alveolatum strigosum, setis crassis flavis; corolla 15–16 mm longa, ligula 1.75 mm lata flava in dorso purpurea, tubo 4 mm longo pubescenti; antherae 4 mm longae; stylus flavus, ramis 3 mm longis nigro-viridis; achaenia uniformia virido-flava 7–8 mm longa 0.6 mm lata in rostro crassiusculo gradatim attenuata 10-costata; pappus albus 5 mm longus 2-seriatus.

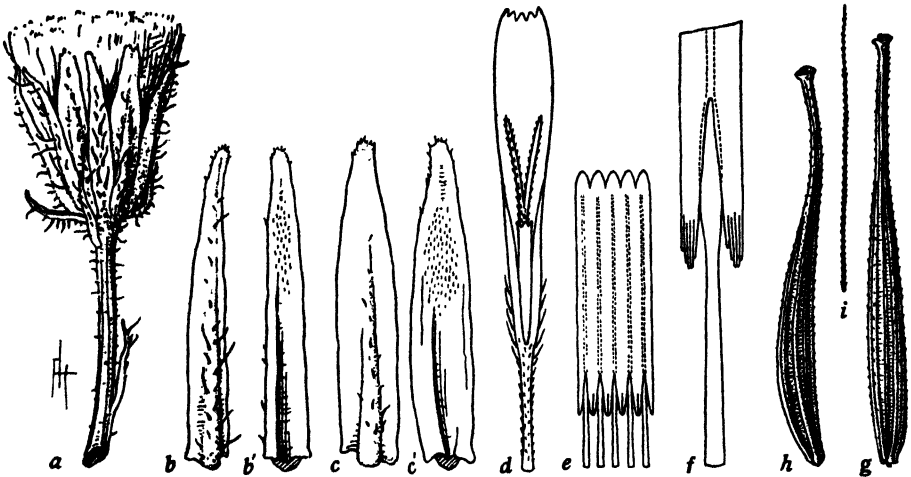


Fig. 283. *Crepis vesicaria proleptica*, from type (K): a, fruiting head, $\times 2$; b, b', c, c', 2 inner involucral bracts, outer and inner faces, $\times 4$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g–i, achenes and pappus seta, $\times 8$.

Plant 5–7 dm high; caudex woody, 0.5–1.5 cm wide; caudical leaves about 30 cm long, 5 cm wide, oblanceolate, acute, sinuate-dentate or lyrate-pinnately parted, gradually attenuate into a long winged petiole; upper cauline leaves lanceolate, acuminate, auriculate-amplexicaul; stem erect, remotely 8–10 branched beginning near base, lower branches elongated, strict, cymosely branched above, forming few-headed open corymbiform clusters; peduncles 3–11 cm long, somewhat thickened near head, hispid with green glandless setules; heads erect, rather large, 50–60-flowered; involucre 11–13 mm long, 6–8 mm wide, cylindric-campanulate, dark green, the dorsal keels and setae of the inner bracts dark green; outer bracts 6–8, lanceolate, acute, $\frac{1}{4}$ – $\frac{1}{3}$ as long as the inner; inner bracts 12–16, strongly nerved and densely pubescent on inner face with coarse shining hairs, becoming carinate dorsally, spongy-thickened near base; receptacle strigose, the trichomes coarse, yellow, shining; corolla 15–16 mm long; ligule 1.75 mm wide, yellow, reddish-purple on outer face; teeth 0.1–0.2 mm long; corolla tube 4 mm long, densely pubescent with papilliform hairs and, near summit and base of ligule, with several-celled acicular hairs up to 0.7 mm long; anther tube 4×1.25 mm dis.; appendages about 0.7 mm long, lanceolate, acute; filaments 0.75 mm longer; style branches 3 mm long, 0.15 mm wide, dark green; achenes greenish-yellow, 6–7 mm long, 0.6 mm wide, 10-ribbed, the beak coarse and definitely ribbed to the apex; pappus 5 mm long, 2-seriate. See pl. 34; fig. 283.

N.W. Morocco, where it is known from only two localities, one certainly and the other probably at a low elevation.

A photograph of the type is in Herb. UC.

This subspecies, like the next, is of special interest because it appears to be a connecting link between the more advanced subspecies, such as subsp. *taraxacifolia* and *typica*, on one hand, and, on the other hand, such primitive species as those comprising sec. 7, particularly *C. achyrophoroides* and the tall, single-stemmed forms of *C. albidu*. It is with the idea that this subspecies represents a transitional stage in the evolution of the genus and, in this sense, that it was preliminary to the more recently evolved forms that it is given the name subsp. *proleptica*. I was at first inclined to recognize it as a species; but the discovery of the very similar subsp. *congenita*, which is evidently hybridizing naturally with subsp. *taraxacifolia*, and the fact that the only other specimen of subsp. *proleptica* known to me besides the type is somewhat atypical, seemed sufficient reason to recognize both subsp. *proleptica* and *congenita*.

As already stated, this subspecies is intermediate between *C. achyrophoroides* of Abyssinia and *C. vesicaria taraxacifolia* of N.W. Africa and S.W. Europe. It also resembles somewhat the taller subspecies of *C. albidu* which are endemic in Spain. Apparently, *C. vesicaria proleptica* represents an intermediate phase in the evolution of subsp. *typica* and *taraxacifolia* and other widespread species the advanced phylogenetic position of which is marked by greater reduction in size of heads, flowers, and fruits, and further specialization of the finely beaked achenes.

The robust appearance of the plants of subsp. *proleptica* naturally suggests that this may be a polyploid species. But in the type the pollen is abundant and the grains are 3-pored, regular in size, averaging about 28μ in diameter. (In two normal plants of subsp. *taraxacifolia* the pollen was 3-pored and averaged $26-28\mu$ in diameter.) In m.v. 78 the pollen is also abundant, but the grains are irregular, ranging from 21 to 32μ and averaging 27μ in diameter. Such irregularity could be caused by either environmental or genetic conditions; the size of the grains seems to indicate that this variant is a diplont, but it may be a hybrid of some sort.

That subsp. *proleptica* shows strong affinity with *C. achyrophoroides* is shown by the habit of the plant, the size and shape of the leaves, the indumentum of leaves, stem, involucre and corolla, and the straw-colored, coarsely beaked achenes. That it is a more advanced form is shown by the more numerous, smaller heads, the reduced outer involucre bracts, the smaller florets and achenes, and the shorter, finer, white pappus. These latter features and the green style branches of subsp. *proleptica* indicate an approach to subsp. *taraxacifolia*.

Morocco: Casablanca Prov., Rabat R., *Grant* in 1888 (K, UCf) type; around Tangier, rich meadows, *Salzmann misit Aug.*, 1825 (K) m.v. 78.

Minor Variant of C. vesicaria proleptica

78. Caudical leaves lyrate pinnately parted, terminal segment rhomboid, subcordate, lateral segments broad, rounded, recurved; involucre with or without dark setules; outer bracts somewhat broader than in the type of the subspecies and with wider scarious margins; corolla 16 mm long; corolla tube pubescent, as in type, except that the acicular hairs at summit of tube and base of ligule are more numerous, coarser, somewhat tortuous, and up to 1 mm long. Otherwise typical. *Salzmann misit*, Aug., 1825 (K), fertile meadows around Tangier, Morocco.

181, *h. Crepis vesicaria congenita* subsp. nov. Herba perennis vel biennis 5–7 dm alta; caudex ligneus 0.5–1.5 cm latus; folia caudicalia 12–30 cm longa 3–7 cm lata, oblanceolata dentata vel subpinnatifida; folia caulina similia vel sessilia amplexicaulia; caulis erectus 8–10-ramosus, ramis inferis elongatis ad summitatem cymose

ramosis; pedunculi 3–11 cm longi stricti vel arcuati hispidulosi; capitula 50–60-flora; involucria 9–11 mm longa 5–7 mm lata pallida; squamae exteriores 6–8 lanceolatae, interiores 12–16 lanceolatae ad maturitatem carinatae et spongioso-incrasatae; receptaculum alveolatum strigosum, setis crassis flavis; corolla 12 mm longa, ligula 1.75 mm lata flava in dorso purpurea, tubo 4–5 mm longo pubescenti; antherae 3.75 mm longae; stylus flavus, ramis 1.75 mm longis flavis; achaenia uniformia fusco-flava 6–7 mm longa 0.5 mm lata in rostro tenuo gradatim attenuata 10-striata; pappus albus 4 mm longus 2–4-seriatus.

Plant 5–7 dm high; caudex woody, 0.5–1.5 cm wide; caudical leaves 12–30 cm long, 3–7 cm wide, oblanceolate, obtuse or acute, sinuate-dentate, gradually attenuate into a long or short winged petiole; upper cauline leaves lanceolate, acute or acuminate, auriculate-amplexicaul; stem erect, remotely 8–10-branched beginning near base, lower branches elongated, strict, cymosely branched above, forming few-headed open corymbiform clusters; peduncles 1–9 cm long, slightly thickened at base of fruiting heads, glabrescent or sparsely setulose with yellow or green glandless setules; heads erect, medium, 50–60-flowered; involucre 9–11 mm long, 5–7 mm wide, pale grayish-green, the dorsal keels of the inner bracts brownish-yellow, setules yellowish-green; outer bracts 6–8, lanceolate, acute, $\frac{1}{4}$ – $\frac{1}{3}$ as long as the inner; inner bracts 12–16, strongly nerved and pubescent on inner face with coarse shining hairs, becoming carinate dorsally, spongy-thickened near base; receptacle strigose, the trichomes coarse, yellow, shining; corolla 12 mm long; ligule 1.75 mm wide, yellow, reddish-purple on outer face; ligule teeth 0.2–0.4 mm long; corolla tube 4–5 mm long, pubescent with stout stalked yellow or hyaline hairs, papilliform at base of tube, increasing to 1 mm long at base of ligule and then several-celled; anther tube 3.75×1 mm dis.; appendages about 0.7 mm long, linear, acute; filaments 0.75 mm longer; style branches 1.75 mm long, 0.15 mm wide, yellow (in some variants 2 mm long, light green); achenes brownish-yellow, 7–8 mm long, 0.5 mm wide, 10-ribbed, the beak finer and less definitely ribbed than in subsp. *proleptica*; pappus 4 mm long, 4-seriate (2-seriate in some variants). See pl. 35; fig. 284.

Spain, at a few localities in the south (Granada Prov. and S. Jaen Prov.) and in the east (Alicante Prov. and Teruel Prov.); 125–1150 m alt.

A photograph of the type is in Herb. UC.

This subspecies is of special interest, first because of its close resemblance to subsp. *proleptica* and, second, because it appears to have hybridized with subsp. *taraxacifolia*, producing amphidiploid derivatives which resemble one or the other of these two subspecies (cf. m.v. 61–63 and 67 under subsp. *taraxacifolia*, and 79–81 below). Unopened florets of some of these forms contain both 3-pored and 4-pored pollen grains which are larger in size than those of the putative parents. In the type of subsp. *congenita* and another specimen from Granada, the pollen is very scanty and irregular in size, but is 3-pored. This condition may be due to a genetic factor for pollen abortion. In the two specimens from Teruel Prov. there is abundant pollen and the grains are regular, 3-pored, and average $30\text{--}31\mu$ in diameter. But in m.v. 67, which is presumably an amphidiploid hybrid, the pollen is abundant and both 3-pored and 4-pored, and the grains vary in diameter from 24 to 34μ , averaging 30μ . This irregularity in the pollen may indicate irregularity in chromosome distribution which would account for the existence of numerous derived forms. These forms are very variable, but they can be referred to one or the other of the two subspecies. Field studies are needed on the present distribution of this subspecies as well as of subsp. *proleptica*.

Spain: Granada, Winkler (Po 17721) type; *ibid.*, Winkler ? (UC); Jaen Prov., Sierra Magina, Golondrina, N. slope, calcareous rocks, 1150 m, Cuatrecasas in 1926 (Bar) m.v. 79; Alicante

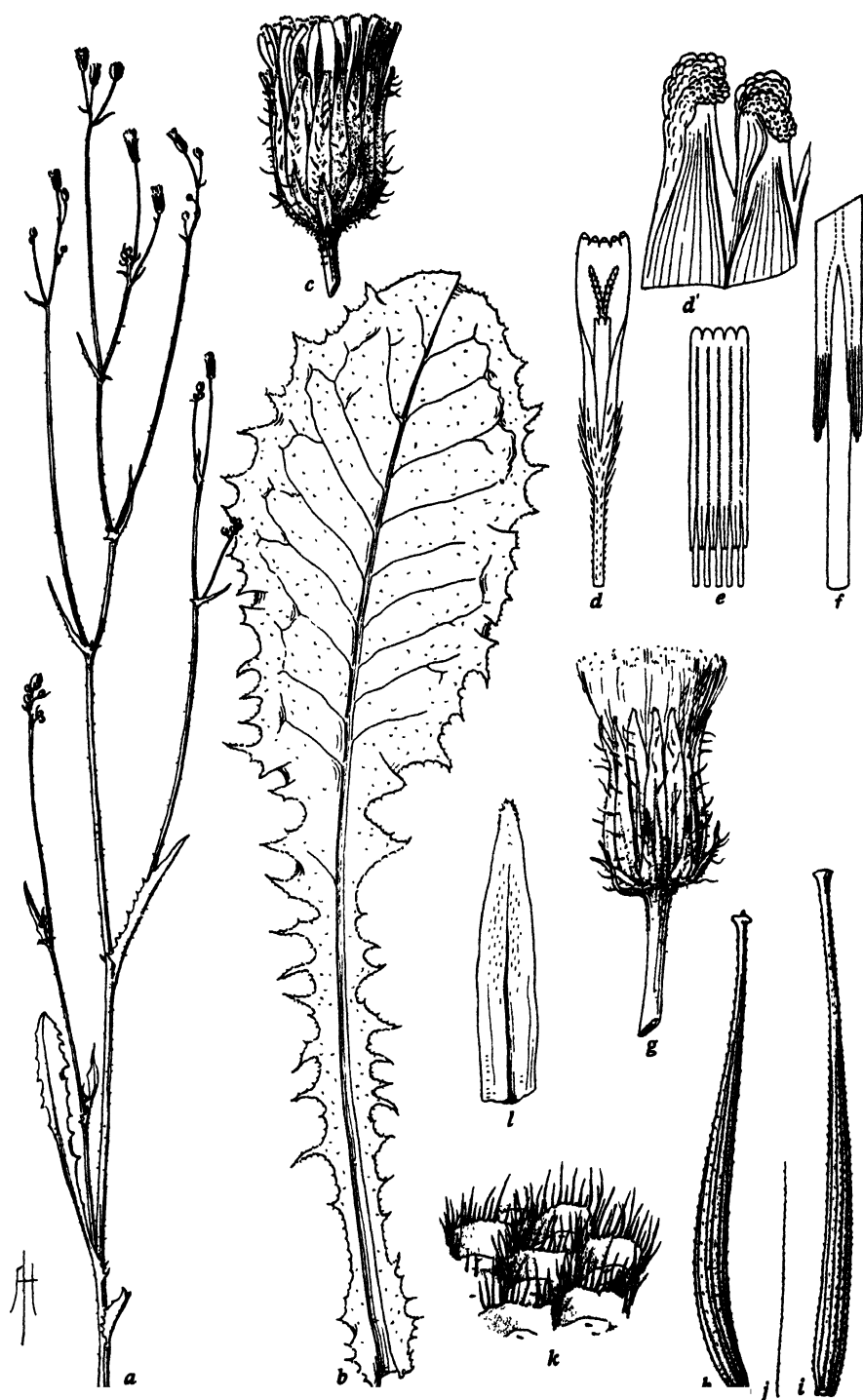


Fig. 284. *Crepis vesicaria congenita*, a-f, from type (Po 17721); g-l, from Winkler (Po 17625): a, part of plant, $\times \frac{1}{4}$; b, basal cauline leaf, $\times \frac{1}{2}$; c, flowering head, $\times 2$; d, floret lacking ovary, $\times 4$; d', detail of ligule teeth, $\times 50$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, fruiting head, $\times 2$; h-j, achenes and pappus seta, $\times 8$; k, detail of receptacle, $\times 25$; l, inner involucre bract, inner face, $\times 4$.

Prov., Mt. Hifac, 125 m, *Font Quer* in 1923 (Bar, UC) as *C. vesicaria* var. *glabrifolia* Fiori ad *taraxacifoliam* *verg.* = m.v. 81; E. Teruel Prov., Penarroja, *Winkler* (Po, Ucf); *ibid.*, Loscos (Po); *ibid.*, Monreal del Campo, *Benedicto* in 1894 (Bar) as *C. taraxacifolia* = m.v. 80.

Minor Variants of C. vesicaria congenita

79. Very robust, although only 5 dm high; caudical leaves lacking; cauline leaves large, deeply pinnatifid with narrow acute lateral segments; involucre sparsely setulose and gland-pubescent, setules short, dark; outer bracts ovate-lanceolate, $\frac{1}{2}$ as long as the inner; corolla 15 mm long; anther tube 4–5 mm long; style branches 2.5 mm long, greenish-yellow; achenes brownish-yellow, 7–8 mm long; pappus 2-seriate. Probably an amphidiploid derivative from subspp. *congenita* \times *taraxacifolia*. The pollen is plentiful and apparently all 3-pored. The grains range from 24 to 32 μ , averaging 29–30 μ in diameter. *Cuatrecasas* in 1926 (Bar), calcareous rocks, 1150 m, N. slope, Golondrina, Sierra Magina, Jaen, Spain.

80. Achenes, as in subsp. *taraxacifolia*, finely beaked and finely ribbed, the involucre rather dark, and the setules on the inner involucral bracts short and dark. Although closely resembling subsp. *congenita* in most respects, yet the characters mentioned above are unmistakable evidence of hybridization with subsp. *taraxacifolia*. The pollen, however, is apparently all 3-pored and too small for a polyploid, ranging from 23 to 30 μ and averaging 26 μ in diameter. Probably this is a diploid hybrid derivative. *Benedicto* in 1894 (Bar), Monreal del Campo, Teruel Prov., Spain.

81. Stem reddish near base; caudical leaves only 10–14 cm long, runcinately dentate or sub-pinnatifid, shortly petioled, glabrate above; involucral setules absent, much reduced or glandular; pappus 2-seriate. The pollen is very irregular, ranging from 23 to 37 μ , and averaging about 30 μ in diameter. Probably some of the largest grains are 4-pored. Presumably another amphidiploid derivative. *Font Quer* in 1923 (Bar, UC, as *C. vesicaria* ad *taraxacifoliam* *verg.*), among herbs, tree-covered slope, Mt. Hifac, "Regno Val." (= Mongo, between Denia and Javea, Alicante Prov.), Spain.

Relationship

Crepis vesicaria *sen. lat.* includes a remarkable array of subspecies and forms. The eight subspecies are at least partly isolated, either geographically or ecologically, except, perhaps, subsp. *proleptica*, about which very little is known. Seven of these subspecies are diploids or have diploid forms, which can be arranged, in ascending order from more primitive to more advanced types, approximately as follows: subspp. *proleptica*, *congenita*, *hyemalis*, *andryaloides*, *taraxacifolia*, *typica*, and *myriocephala*. The hybrid swarm, including amphidiploids, which has been designated subsp. *stellata*, is of course more advanced chronologically than its putative parents, subspp. *taraxacifolia* and *myriocephala*, although it is for the most part intermediate between them morphologically. The most primitive subspecies, *proleptica* and *congenita*, exhibit marked resemblances to *C. achyrophoroides* and the tall forms of *C. albida*, both of sec. 7. Subsp. *hyemalis* is more primitive than subsp. *taraxacifolia* and may be considered as intermediate between it and subsp. *typica*, on one hand, and *C. Clausonis* and *C. spathulata*, on the other. Similarly, subsp. *andryaloides* may be considered as intermediate between subsp. *taraxacifolia* or subsp. *typica* and *C. divaricata* or *C. canariensis*.

Thus, *C. vesicaria* *sen. lat.* includes forms which show some affinity with species in one of the more primitive sections of the genus, and others which approach the most advanced species in this section, *C. Marshallii*. The allocation of a phylogenetic position in this section to *C. vesicaria*, therefore, is purely arbitrary. On the basis that its most advanced forms, comprising subsp. *typica*, reveal the high degree of advancement which has been reached in this inclusive species, it has been placed next to *C. Marshallii*.

182. *Crepis Marshallii* (C. A. Mey.) F. Schultz

Flora 23: 718. 1840. (Fig. 285.)

Biennial, 3–8 dm high; root straight, tapering, woody; caudex slightly swollen, marked with scars of old leaves, leafy above; caudical leaves up to 18 cm long, 3.5 cm wide, spatulate or oblanceolate, acute or obtuse, dentate to lyrate-runcinate-

pinnatifid with large truncate terminal segment and triangular acute lateral segments, attenuate into a long or short winged petiole with broader clasping base, hispidulous with short pale glandless hairs or glabrescent; lower cauline leaves similar, middle ones lanceolate, acuminate or acute, sessile, subamplexicaul or amplexicaul-auriculate, \pm lacinate, upper ones gradually reduced, bractlike, uppermost linear, brown-scarious; stem erect, robust, 3–6 mm wide near base, sulcate or striate, fistulose, finely hispidulous or glabrescent, branched above or from near base, branches strict or slightly arcuate, corymbiform, 1–13-headed; peduncles 2–7 cm long, arcuate, striate, somewhat thickened in fruit, like involucre shortly and finely gland-pubescent; heads medium to small, many-flowered; involucre cylindric-campanulate, 10–12 mm high, 4–5 mm wide in fruiting heads; outer involucre bracts 7–9, with 1 or 2 subtending, $\frac{1}{3}$ – $\frac{1}{2}$ as long as inner bracts, lance-linear or linear, obtuse, white-ciliate at apex, pale brown below, purplish near apex, somewhat ribbed or rugose, membranous-margined, becoming scarious and lax; inner involucre bracts 12–14, lanceolate, obtuse, white-ciliate at apex, in 2 series, the inner ones broader and membranous-margined, densely appressed-pubescent on inner face with yellowish shining hairs, becoming rounded-carinate and spongy-thickened, the carina finely striate, densely gland-pubescent with short stout hairs dark at base and pale above, glands brown; receptacle convex in fruit, alveolate-fimbriate, alveoles 0.5 mm wide, fimbriae low, membranous, white-ciliate, cilia stout, 0.25 mm high; corolla 10 mm long; ligule 1 mm wide, pubescent dorsally on lower half with acicular hairs 0.2–0.3 mm long; ligule teeth 0.15–0.3 mm long, triangular, acute; corolla tube 3 mm long, very slender, densely pubescent with stout acicular hairs 0.05–0.1 mm long; anther tube 3×0.8 mm dis.; appendages 0.5 mm long, lanceolate, acuminate, united; filaments 0.7 mm longer; style branches 1.25–1.75 mm long, 0.7 mm wide, green; achenes pale brown, very slender, 6–8 mm long, the body 3 mm long, 0.4 mm wide, fusiform, narrowed at the pale-calloused hollow base, gradually attenuate into the filamentous beak 3–5 mm long with expanded pappus disk, 10-ribbed, ribs narrow, rather prominent, rounded, finely barbellulate; pappus yellowish-white, 5 mm long, 2-seriate, very fine, soft, deciduous. Flowering May; flowers yellow, purplish on outer face of ligules. Chromosomes (m.v. 2), $2n = 8$.

Barkhausia Marschallii C. A. Mey., Ber. Kais. Acad. Wiss. St. Petersburg. 57. 1831.

Crepis taurinensis Bieb., Fl. Taur. Cauc. 3: 537. 1819 excl. syn. praeter Bieb. *vide* DC. et Ledeb.

C. biennis Pall., Ind. Taur., et Bieb., Fl. Taur. Cauc. 2: 257 excl. syn. praeter Pall. et Bieb. *vide* Ledeb. et DC.

Hieraciodes Marschallii O. Kuntze, Gen. 1: 346. 1891.

S. Russia, in the Crimea, the Caucasus, and W. Caspian regions, fields and waste places. The authentic specimen of Meyer, Enum. Cauc. Casp. n. 456 in herb. Boissier, is taken as the type of the species. A photograph is in Herb. UC. From the title of Meyer's paper (*loc. cit.*) the type locality is the region to the west of the Caspian Sea.

Caspian Region: "toward the Caspian Sea," Meyer 456 (Bo, UCf) type; *ibid.*, without locality (DC, B); at Caspian Sea, near Kislagatish, meadows and shady places, Hohenacker in 1836 (G, P, K, Mo, NY, CA, US, UCf). **Transcaucasia:** Azerbaidzhan, near Kjudamir, abandoned field, Isaev in 1936 (NY); Iberia (= Georgia), Steven in 1820 (DC, UCf); Iberia, Wilhelms in 1824 (K); locality uncertain, Radde 2533 (BB) m.v. 1. **Crimea:** locality 1, Balbis (DS).

Minor Variants of C. Marschallii

1. Leaves, stem, and involucre glabrescent or only tomentulose. Radde 2533 (BB), locality uncertain, Caucasus.

2. Achenes 5–6 mm long, beak 2–3 mm long. Known only from garden plants grown from seed received from Tiflis, Georgia. It is uncertain whether this seed was collected in the wild or came from a botanic garden. These plants have the characteristic gland-pubescent on peduncles and



Fig. 285. *Crepis Marshallii*, *a-k*, from type (Bo); *l*, from *Hohenacker* in 1836 (G); *m*, from hort. genet. Calif. 1532 (grown from seeds received from G. Woronoff, Tiflis; cf. UC 517905): *a*, plant, $\times \frac{1}{4}$; *b*, flowering head, $\times 2$; *c*, fruiting head, $\times 2$; *d*, *e*, 2 inner involucre bracts, outer and inner face, $\times 4$; *f*, floret lacking ovary, $\times 4$; *f'*, detail of ligule teeth, $\times 50$; *g*, anther tube, $\times 8$; *h*, detail of appendages, $\times 32$; *i-k*, 2 achenes and a pappus seta, $\times 8$; *l*, detail of receptacle, $\times 25$; *m*, somatic chromosomes, $n = 4$, $\times 1250$.

involucres and the floral characters are similar. The shorter achenes may be characteristic of a local race of this species. This is indicated by the fact that in the specimen of Wilhelms (cited above) the achenes are only 5.5–6.5 mm long and otherwise typical. Ex hort. genet. Calif. 1532 and 3175 (UC).

Relationship

Crepis Marschallii is close to *C. vesicaria*. It resembles subsp. *taraxacifolia* in the narrow outer involueral bracts and uniform achenes; but the achenes are much narrower and more finely beaked. It resembles subsp. *typica* in that the outer involueral bracts are lax and scarious like the bracts subtending the branches of the inflorescence, but the achenes of *C. Marschallii* are of a much more advanced type. The geographic area of *C. Marschallii* is widely separated from that of *C. vesicaria*, since the latter does not extend farther eastward than Thrace. But the karyotypes of the two species are practically identical. It is obvious, therefore, that *C. Marschallii* was derived from the same ancestral stock as *C. vesicaria*. This parent form probably occurred in Iran, and it may be represented in that region today by the closely related *C. elymaitica* of sec. 7. However, *C. achyrophoroides*, also of sec. 7, is much closer morphologically to *C. vesicaria* than is *C. elymaitica* (cf. subsp. *proleptica* and subsp. *congenita*). It is very probable that *C. achyrophoroides* formerly existed in Iran but was unable to withstand the increasing desiccation of that region, whereas it was able to maintain itself under more favorable conditions in Abyssinia. In marked contrast is the advanced and specialized *C. Marschallii* which has been collected on the arid western shores of the Caspian Sea.

SECTION 26. NEMAUCHENES

The 7 species comprising this section consist of annual plants which are mostly precocious and obviously adapted to xerophytic conditions. In addition to the slender ephemeral root, few basal leaves, and divaricate branches, the group as a whole is characterized by the medium or small flower heads, the setaceous involucre with short outer bracts, and, except in *C. setosa* subsp. *typica*, by the biform achenes. The most primitive member of the group is *C. juvenalis*, since it has the

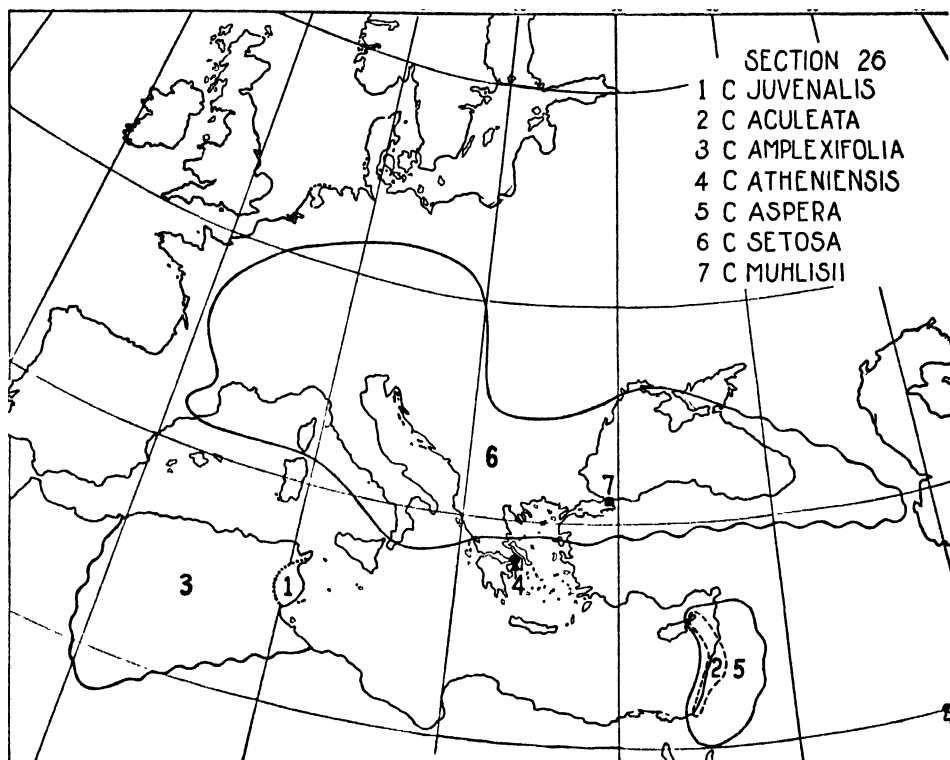


Fig. 286. Geographic distribution of the 7 species in sec. 26. Species no. 4 and no. 7 are each known only from 1 station. Based on Goode Base Map No. 124. By permission of the University of Chicago Press.

largest heads and achenes and the inner achenes are scarcely beaked. It is endemic in Tunisia (cf. fig. 286). Next is *C. aculeata* with its large marginal achenes and long-beaked inner achenes. It is endemic near the coast of the E. end of the Mediterranean. *C. amplexifolia* stands next; although it is very distinct from *C. aculeata* in many characters, the achenes of the two are similar, except that those of *C. amplexifolia* are much smaller. It is widely separated from its closest relative, being distributed from Tripoli to W. Morocco and southward from the Mediterranean coast at least as far as Tauorirt, a distance of more than 400 km. *C. atheniensis*, although known only from the type specimen, presents such a combination of the characters common to this group that it cannot be explained as a natural hybrid or as a form derived in later generations from hybridization between any two of the three species which it most resembles, viz., *C. aculeata*, *C. amplexifolia*, and *C. aspera*. It seems much more probable that it descended from an ancestor in common with the other species of this section, and that it was adventive in Athens, having

been brought there from its native area, perhaps from some island in the E. Mediterranean or some isolated area in Asia Minor. *C. aspera* was placed in the genus *Endoptera* by de Candolle (178), along with *C. Dioscoridis*, mainly because of the similarity in shape of the peculiar marginal achenes of these two species. But it is obviously a member of this section, resembling *C. amplexifolia* in habit and leaves and in the ovate outer involucre bracts, but differing strikingly in its achenes. *C. aspera* is confined to the E. end of the Mediterranean. *C. setosa*, the only very widespread species in this section, differs from all the other species in having uniform beaked achenes, except in its very local subsp. *Topaliana* of N. Greece. In this subspecies, however, the marginal achenes resemble those of *C. atheniensis* and *C. Muhlisii*. All of the more primitive species in this genus have uniform achenes; and *C. setosa* subsp. *typica* has retained this characteristic, whereas subsp. *Topaliana* not only has biform achenes but is much more reduced in size throughout all parts of the plant. The most advanced species in this section, as determined by its extreme reduction in size, is *C. Muhlisii*, which, like *C. atheniensis*, is known only from the type locality, which is near Scutaria, Turkey. It finds its closest relative in *C. setosa* *Topaliana*, from which it is very distinct. Four of the five specimens seen by me have very peculiar abnormal anthers which nevertheless appear to produce good pollen.

This section, like secs. 23–25, has had its development in the Mediterranean region (cf. fig. 286). But the present distribution of the more primitive species on an east–west axis would appear to indicate that they were more widely distributed to the east in earlier times. At any rate, this idea is consistent with the general hypothesis (developed in Part I) of a Central Asiatic origin for the genus.

Key to the Species of Section 26

Inner involucre bracts 7–8.

Inner involucre bracts with a median row of short black setae, glabrous on inner face; outer bracts lance-linear; corolla tube glabrous; ligule yellow without red on outer face; achenes dimorphic, dark brown. Tunisia.....183. *C. juvenalis*, p. 869

Inner involucre bracts with long yellow or brown setae or sometimes glabrous, pubescent on inner face; outer bracts ovate or lanceolate; corolla tube pubescent; ligule yellow with red on outer face; achenes biform or uniform, pale brown, E. Mediterranean.....187. *C. aspera*, p. 878

Inner involucre bracts 10–14.

Outer bracts 5, very short; inner achenes with 16–18 ribs.....184. *C. aculeata*, p. 871

Outer bracts 10–14, from $\frac{1}{4}$ to $\frac{1}{2}$ as long as the inner bracts; inner achenes with 10 ribs.

Involucres gland-pubescent, sometimes with short black glandular setules, never with yellow glandless setae. Algeria, Tunisia, and Tripolitania. 185. *C. amplexifolia*, p. 873

Involucres setose or setulose, the setae or setules yellow, without glands.

Stem, branches, or peduncles more or less hispid, setose, or setulose; middle cauline leaves usually lacinate at the base; achenes uniform or, if biform (subsp. *Topaliana*), then the inner achenes pale tawny or yellowish. 188. *C. setosa*, p. 882

Stem, branches, and peduncles glabrous or tomentulose; middle cauline leaves entire or auriculate; achenes biform, the inner ones tawny or deep tawny.

Involucres 6–7 mm long, 3–4 mm wide; inner involucre bracts white-pubescent on inner face; achenes about 3 mm long. Asia Minor (Scutari).....189. *C. Muhlisii*, p. 886

Involucres 9–10 mm long, 5–6 mm wide; inner involucre bracts yellow-pubescent on inner face; achenes 4.5–6.5 mm long. Greece (Athens).....186. *C. atheniensis*, p. 876

183. *Crepis juvenalis* (Delile)F. Schultz, *Flora* 23: 719. 1840. (Fig. 287.)

Annual, 0.8–3.5 (mostly 1–2.5 dm high); root slender; caudex \pm swollen, leafy, several-stemmed; caudical leaves 4–15 cm long, 1–3 cm wide, oblanceolate, acute, runcinately dentate or pinnatifid to pinnately parted with narrow acute denticulate segments, attenuate into a winged petiole, canescent-tomentulose or glabrescent; lower cauline leaves similar, middle and upper ones sessile, auriculate-amplexicaul, uppermost bractlike; stems semidecumbent, terete, fistulose, striate, canescent-tomentose near base, cymosely 3–5-branched, branches remote, the lower elongated, 2–3-branched, the upper pedunculate; peduncles 0.5–10 cm long, arcuate, notably swollen toward summit but constricted just below fruiting heads, tomentose or tomentulose; heads erect, medium, 50–70-flowered; involucre cylindric-campanulate, 10–13 mm long, 4–8 mm wide in fruit, canescent-tomentose; outer bracts 6–10, about equal, $\frac{1}{4}$ – $\frac{1}{3}$ as long as the inner in mature heads, lance-linear, acuminate, pale-scarious, lax, sometimes with a median row of small setae; inner bracts usually 8, lanceolate, acute, with a median row of short black setae, glabrous on inner face, membranous margined, becoming strongly navicular and spongy-thickened, infolding marginal achenes, ultimately half-reflexed; receptacle areolate-fimbrillate, areolae white with black central stipe, fimbrillae low, yellowish, fleshy, densely ciliate, cilia white, 0.5 mm long; corolla 14 mm long; ligule 1.5 mm wide; teeth 0.5 mm long; corolla tube 4 mm long, glabrous; anther tube 3.5×1.25 mm dis.; appendages about 0.6 mm long, linear, acuminate; filaments 0.5 mm longer; style branches 1.5 mm long, 0.1 mm wide, yellow; achenes dark brown, biform; marginal achenes 5–7.5 mm long, 0.5–0.7 mm wide, gradually attenuate to the narrow apex, constricted at the calloused base, with oblique basal scar, somewhat flattened ventrally and more strongly striate, strongly convex or carinate dorsally and weakly striate, white-pubescent, more densely on ventral face; inner achenes 5.5–9 mm long, 0.3–0.4 mm wide, gradually attenuate into a beak 0.15–0.25 mm wide near apex, with abruptly expanded pale pappus disk, narrowed to the pale-calloused oblique hollow base, 10-ribbed, ribs narrow, rounded, finely spiculate; pappus white, 4–6 mm long (shorter on marginal achenes), 3–4-seriate, setae unequal, outermost shorter and finer, the coarsest about 30μ wide at base, soft, persistent. Flowering March–April; flowers yellow. Chromosomes, $2n = 8$.

Barkhausia juvenalis Delile, Ind. Sem. Hort. Monsp. 23. 1836.

Crepis tunetana Batt., Bull. Soc. Bot. Fr. 59: 421. 1912.

Endemic in Tunisia, where it occurs in a rather wide range of environmental conditions, from locations near the sea on the N.E. promontory south of Cape Bon to the central arid uplands near the Algerian border (at elevations of at least 500–1000 m) and to the semidesert region between Sfax and Gabes. As might be expected, specimens from these different regions exhibit considerable variation in size of the whole plant, but otherwise they are very uniform except for the slight variations recorded in the above description. It is noteworthy that some of the marked differences in size of plant appear to be inherited. This is indicated by the close similarity in stature of the original plants—those collected by Chabrolin on the Mahouin Pen. south of Cape Bon (hort. genet. Calif. 3206) and near Kairouan (3207)—and their cultivated progenies.

The type, in Herb. Monspeliensis, was collected about 1836 by Delile in the old city of Montpellier near Port-Juvénal, whence came the name of the species. In Thellung's "*La Flore adventice de Montpellier*," published in 1912, he states: "*Patrie toujours inconnue*," and suggests that it will be necessary to search in N.

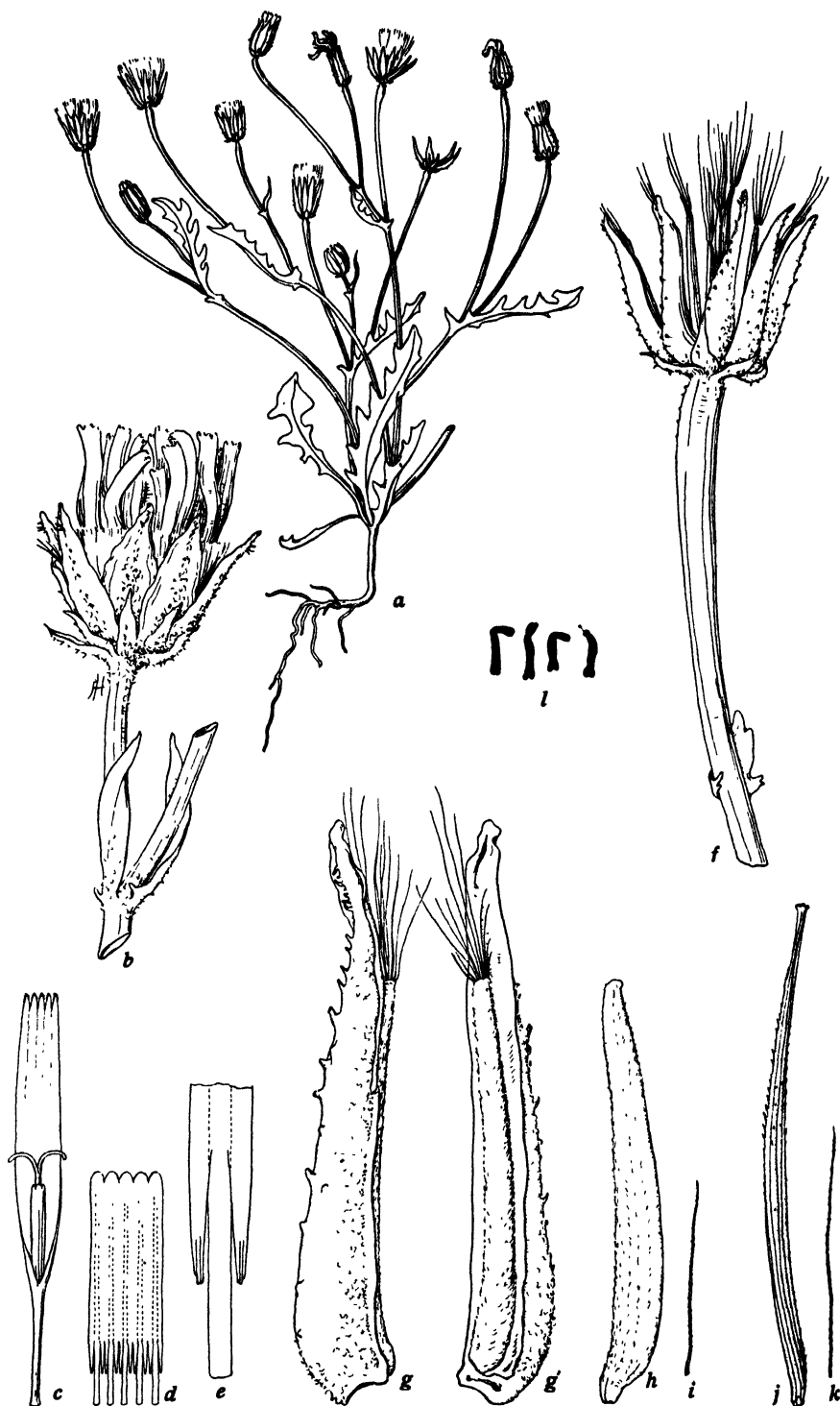


Fig. 287. *Crepis juvenalis*, a-k, from type (Ms) and isotype (UC 296069); l, from hort. genet. Calif. 3205 (grown from seeds collected in Tunisia by Dr. Ch. Chabrolin; cf. UC 482467): a, plant, $\times \frac{1}{2}$; b, head, after anthesis, $\times 2$; c, floret lacking ovary, $\times 4$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, fruiting head, $\times 2$; g, g', inner involueral bract enclosing marginal achene, $\times 8$; h, i, marginal achene and a pappus seta, $\times 8$; j, k, inner achene and a pappus seta, $\times 8$; l, somatic chromosomes, $n = 4$, $\times 1250$.

Africa or the Near East where such nearly related species as *C. amplexifolia* occur. That same year Battandier published his *C. tunetana*, citing fields around Sfax as its habitat. Although it is unfortunate that Battandier's name cannot stand, yet it is of some interest that the species was named and described as an introduced weed nearly a century before its native habitat was known. One small spec. in Herb. Missouri Bot. Gard. (Mo 119591), collected by Muschler at Luksor, Egypt, in 1904 is certainly this species, and it may have been adventive there. The plant has also been reported as adventive in the Canary Islands (Webb et Berth., Phyt. Canar. 3: 459. 1836–1850). A photograph of the type and an isotype are in the herbarium of the University of California (Berkeley).

Tunisia: Sfax, olive orchard to the south, Battandier in 1909 (UC, Ms, Alger) as *C. tunetana*; Sfax dist., route from Sfax to Triaga, entrance to olive plantation among cereals, Chabrolin in 1932 (UC); between Sfax and Gabes, Bled Thola, Forêt de Gommiers (*Acacia tortilis*) "abundant," Chabrolin in 1935 (UC); W. uplands, Sbeitla, near Feriana, Chabrolin in 1932 (UC); E. plains, Pavilliers, near Kairouan, Chabrolin in 1932 (UC); ex hort. genet. Calif. 34.3207–7, cult. from seeds taken from preceding spec. (UC); Mahouin Pen., Bir Drassey, between Nabeul and Kelibia, Chabrolin in 1932 (UC); ex hort. genet. Calif. 34.3206–10, cult. from seeds taken from preceding spec. (UC).

Relationship

Crepis juvenalis is certainly the most primitive species in this section. It most nearly resembles *C. aculeata* and, although the corolla is about the same length and actually narrower and the anther tube similar to *C. aculeata*, yet it has larger flower heads and much less attenuate achenes than that species.

184. *Crepis aculeata* (DC.) Boiss.

Fl. Orient. 3: 856. 1875. (Fig. 288.)

Annual, 1.5–4.5 dm high; root straight, woody; caudex short, swollen, leafy; caudical leaves withering, persistent, up to 15 cm long, 3.5 cm wide, lanceolate or oblong, equally attenuate to apex and base, obtuse-mucronate or acute, denticulate to runcinate-pinnatifid, terminal segment sometimes $\frac{1}{3}$ – $\frac{1}{2}$ as long as whole leaf, sometimes small, lateral segments short or extending nearly to midrib, denticulate, rarely bipinnate, corneous-mucronate, canescent-tomentulose, puberulent or glabrescent; lower cauline leaves similar, middle ones sessile, acutely auricular, uppermost bractlike; stem erect, sinuate, branched from near base, branches divaricate, arcuate, longer than axis, forming a spreading cymose-corymbiform bushlike plant, canescent-tomentulose below and at bifurcations, glabrous above or sparsely setulose; peduncles 1–15 cm long, slender below, broader above, slightly constricted below head, fistulose, \pm tomentulose; heads erect, medium, many-flowered; involucre cylindric, 10–12 mm long in fruit, 5–7 mm wide, canescent-tomentulose, armed with strong spiny bristles on inner bracts, remaining erect or slightly reflexed; outer bracts 5, very short, lance-linear, acute, becoming lax; inner bracts 10–12, lanceolate, obtuse, ciliate at tip, scarious-margined, rarely lacking the dorsal median row of strong bristles, ventrally densely pubescent with short shining hairs, becoming dorsally keeled, spongy-thickened near base, infolded, clasping the achene; receptacle alveolate, glabrous; corolla 12–13 mm long; ligule 2.75 mm wide; teeth 0.75–2 mm long; corolla tube 3.5 mm long, pubescent with very short 2-celled hairs; anther tube 3×1.25 mm dis.; appendages 0.6 mm long, oblong, obliquely obtuse with a small claw; filaments extremely short; style branches 2 mm long, narrow, yellow; achenes biform; marginal yellowish or brownish, 8–9 mm long, laterally \pm compressed, oblong or dorsally convex toward base, gradually attenuate to summit, with scanty unequal pappus, dorsally striate, ventrally smooth or with a narrow median wing, with large oblique basal scar and yellow callosity, pubescent

with short white appressed hairs; inner achenes tawny, 5.5–7 mm long, fusiform, attenuate into a rather coarse beak nearly equal to body, body 3–4 mm long, beak 2–4 mm long, pappus disk definitely expanded, base narrow, 16–18-ribbed, ribs

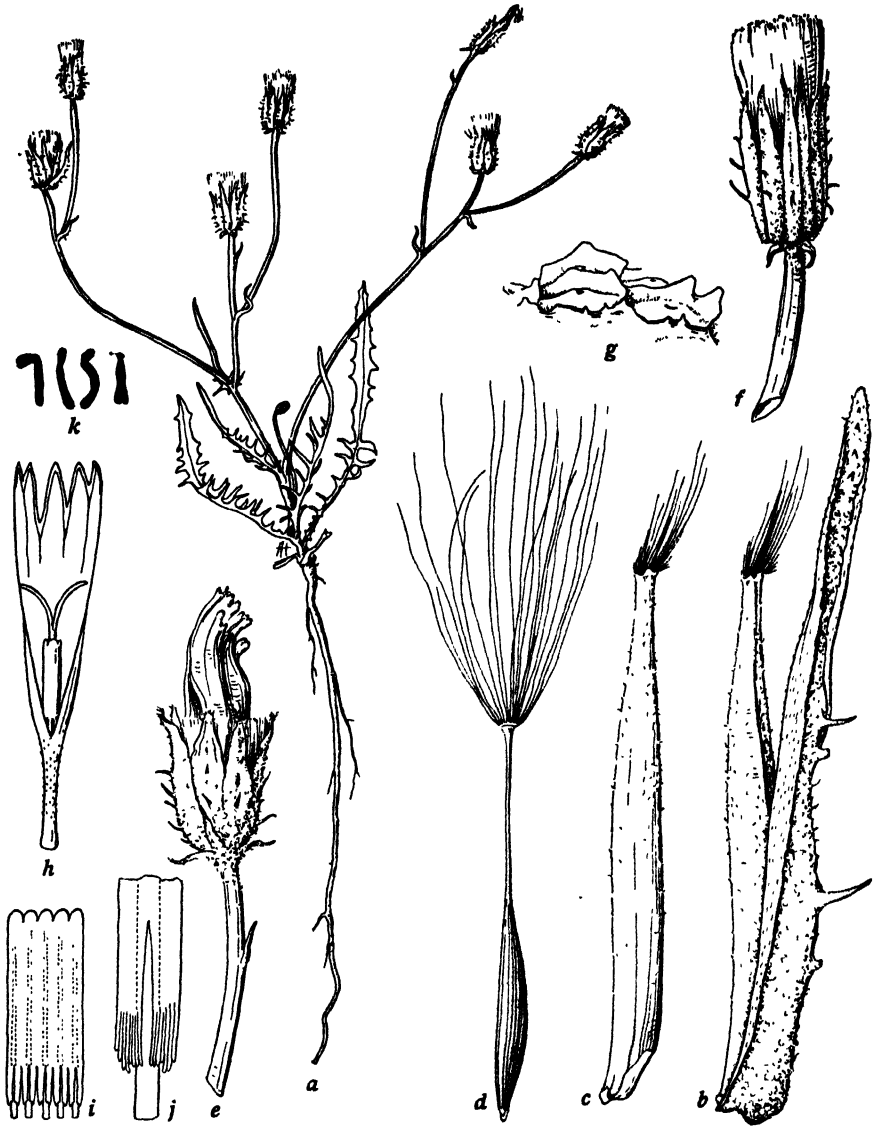


Fig. 288. *Crepis aculeata*, a–d, from type (DC); e–k, from hort. genet. Calif. 1602 (UC 313849): a, plant, $\times \frac{1}{2}$; b, inner involucre bract with marginal achene *in situ*, $\times 8$; c, the same achene removed, $\times 8$; d, inner achene, $\times 8$; e, f, immature and mature heads, $\times 2$; g, detail of receptacle, $\times 25$; h, floret lacking ovary, $\times 4$; i, anther tube, $\times 8$; j, detail of appendages, $\times 32$; k, somatic chromosomes, $n = 4$, $\times 1250$.

fine, with 3–4 somewhat stronger ones, finely spiculate; pappus white, 5–6 mm long on inner achenes, 2-seriate, united at base, fairly strong, persistent. Flowering April–May; flowers golden yellow, ligule teeth purple dorsally. Chromosomes, $2n = 8$.

Endoptera intermedia Boiss. et Bl., ex Boiss., Diag. Pl. Orien. nov. ser. 2, 3: 99. 1856.

Barkhausia aculeata DC., Prod. 7: 159. 1838.

Hieraciodes aculeatum O. Kuntze, Gen. 1: 345. 1891.

E. Mediterranean reg. from the Egyptian-Palestine frontier to Syria and Cyprus; frequent along the coasts in sandy soil; Jordan Valley in Palestine.

The type, without definite locality, in herb. DC. Prod. VII: 159 n. 39, agrees with the descriptions of de Candolle and Boissier.

Cultivated strains of this species exhibited marked variations in habit, in shape and color of the leaves, and in time of flowering. In a strain from S. Palestine the plants were early, low, and spreading; whereas a strain from Syria was later, taller, and more upright, with a definite central axis. This suggests the possibility of a north-south cline, as in *C. capillaris*; but the available data are too scanty to reveal the actual nature of the species.

Syria: Beirut, *Labillardiere* (DL, UCf); *ibid.*, Zohary in 1931 (UC); Saida, *Barbey 574* (Ms, UCf, B, RB). **Cyprus:** Yalussa, *Sintenis et Rigo 284* (K) m.v. 1. **Palestine:** *Aaronsohn 1128* (Ms, UCf); Sharon Plain, Ein-Hai, *Eig* in 1925 (HU, UC); Tira, coast, *Eig* in 1925 (UC); Tel-Aviv, *Eig* in 1922, 1926 (HU); Raffa, *Eig* in 1925 (HU); Jaffa, *Bornmüller 985* (K, B, DL) m.v. 1; Egyptian frontier, between Rapah and Gaza, ex hort. genet. Calif. 1602, cult. from seeds sent by D. Fathi, El Giza (UC).

Minor Variant of C. aculeata

1. (*C. aculeata* var. *Bornmülleri* Huter, Oesterr. Bot. Zeitschr. 57: 114. 1907.) Nearly or quite devoid of the typical spiny bristles on involucre and stem; often depauperate plants. *Sintenis et Rigo 284* (K) Yalussa, Cyprus; *Bornmüller 985* (K, B, DL) Jaffa, Palestine.

Relationship

C. aculeata is closest to *C. juvenalis*, from which it is very distinct in the smaller heads with the characteristic long spines on the inner involucre bracts, in the paler marginal achenes and the inner achenes definitely beaked, in the shorter florets with much wider ligules and longer ligule teeth, in shape of leaves, and in other characters. It is less close to *C. aspera*, with which it will cross and produce partly fertile hybrids, and still less close to *C. amplexifolia*.

185. *Crepis amplexifolia* (Godr.) Willk.

Ex Willk. et Lange, Prod. Fl. Hisp. 2: 272. 1870. (Fig. 289.)

Annual, 1.5–4 dm high; root slender; caudex \pm swollen, up to 1 cm wide, leafy, 1–6-stemmed; caudical leaves up to 12 cm long, 3.5 cm wide, oblanceolate, acute, denticulate to pinnatifid, the teeth or lobes corneous-mucronate, attenuate into a usually short winged petiole, puberulent or glabrescent, \pm ciliate on margin; cauline leaves numerous, mostly small, triangular, lanceolate or linear, acute or acuminate, dentate to deeply pinnatifid with narrow acute lobes, truncate or cordate at the amplexicaul base; stem or stems erect or sometimes decumbent, paniculately branched from near the base, branches strict or arcuate, cymosely 3–4-branched above, forming a loose subcorymbiform aggregate inflorescence, canescent-tomentulose and usually setulose near the base with yellow glandless setules, sometimes shortly gland-pubescent; peduncles 0.5–5 or occasionally 7–9 cm long, slender, arcuate, tomentose, often gland-pubescent, sometimes slightly thickened near head in fruit; heads erect, small or medium, many-flowered; involucre in fruiting heads 7–11 mm long, 4–7 mm wide at middle, urceolate-campanulate, canescent-tomentose, finely gland-pubescent or with short black glandular setules; outer bracts about 10, $\frac{1}{4}$ – $\frac{1}{3}$ as long as the inner bracts, lanceolate, acuminate, membranous-margined, becoming lax and scarious; inner bracts 13, lanceolate, acute or obtuse, white-ciliate at apex, membranous-margined, pubescent on inner face, becoming strongly carinate and spongy-thickened dorsally, infolding marginal achenes, ultimately spread horizontally or completely reflexed; receptacle areolate or alveolate, fimbriae low, somewhat fleshy, finely white-ciliate or glabrescent;

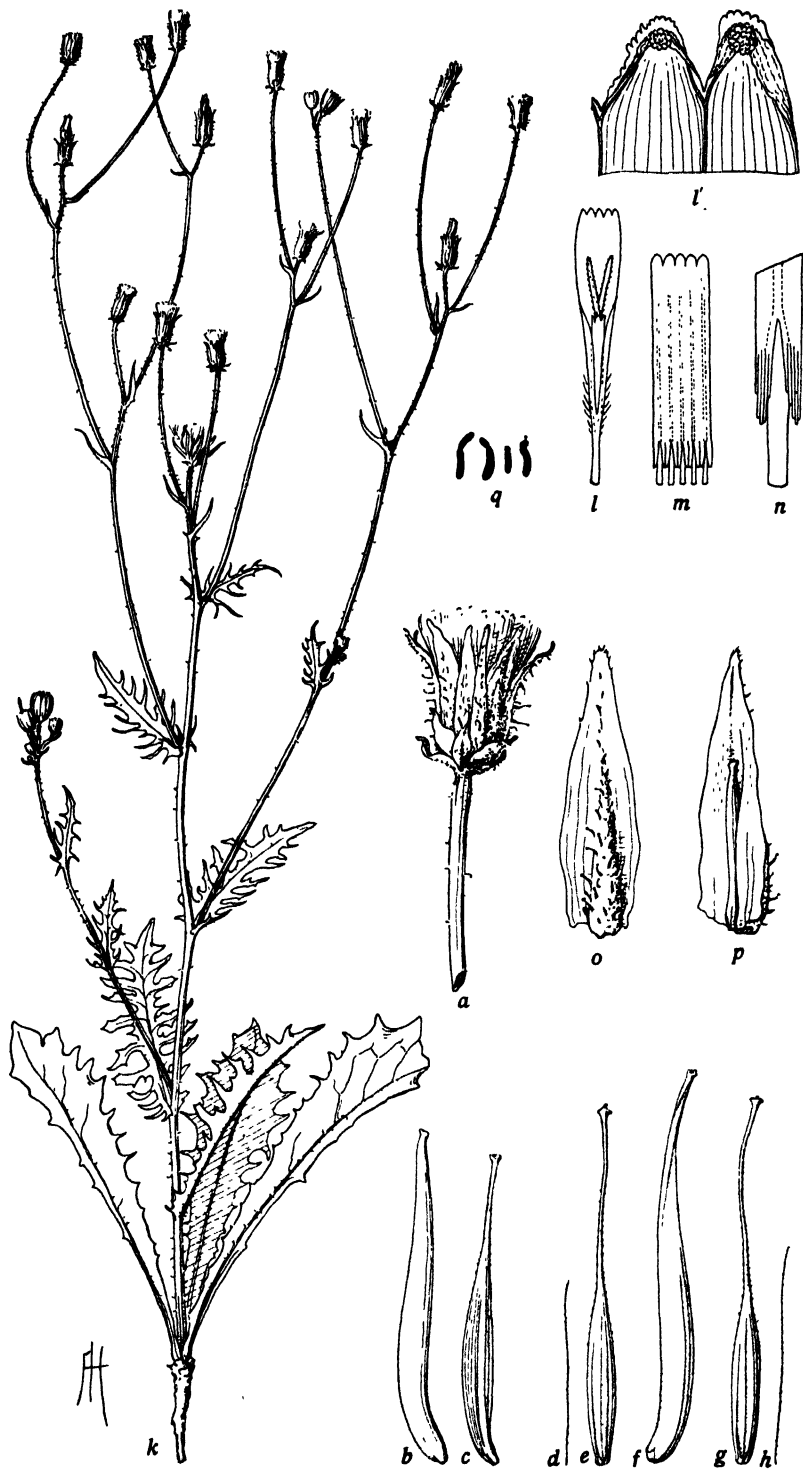


Fig. 289. *Crepis amplexifolia*, a-e, from Battandier in 1889 (UC 429461); f-h, from Batt. et Trab. 552 (Rome); k-q, from hort. genet. Calif. 31.1019-10 (UC 540729): a, head, $\times 2$; b-e, achenes and pappus seta, $\times 8$ (achenes not fully mature); f-h, mature achenes and pappus seta, $\times 8$; k, plant, $\times \frac{1}{2}$; i, floret lacking ovary, $\times 4$; l, detail of ligule teeth, $\times 50$; m, anther tube, $\times 8$; n, detail of appendages, $\times 32$; o, p, inner involucre bracts, $\times 4$; q, somatic chromosomes, $n=4$, $\times 1250$.

corolla 6–9 mm long; ligule 1.25–1.5 mm wide, pubescent at base; teeth 0.1–0.25 mm long; corolla tube 2–3 mm long, pubescent at summit with acicular hairs 0.05–0.5 mm long; anther tube (2.2)3.5 × 0.8(1) mm dis.; appendages 0.4–0.5 mm long, lanceolate, acute; filaments 0.25 mm longer; style branches 1–2 mm long, 0.1 mm wide, green; achenes bifurciform, the marginal beakless, the inner ones beaked; marginal achenes white, 4–6.5 mm long, 0.4–0.5 mm wide dorsoventrally, laterally compressed, gradually attenuate from base to apex or with a very short beak, ventrally smooth, dorsally striate and sometimes spiculate, with oblique basal scar; inner achenes tawny, (3.5)4.5–6 mm long, 0.3–0.5 mm wide, the body subterete, fusiform, abruptly attenuate into a fine beak of about equal length, with expanded pappus disk, finely calloused at the narrow hollow base, 10-ribbed, ribs narrow, rounded, finely spiculate; pappus white, 3–5 mm long, 1-seriate, very fine, soft, caducous. Flowering March–June; flowers yellow, the ligule teeth dark purple, marginal florets purple on outer face of ligule. Chromosomes, $2n = 8$.

Barkhausia amplexifolia Godr., Mem. Acad. Sci. Lett. Montpellier Sect. Med. 1: 437. 1853.

B. amplexicaulis Coss. et Durieu, ex Cosson, Ann. Sci. Nat. ser. 4, 1: 232. 1854 non *C. amplexicaulis* Schur.

The type, in Herb. Monspeliensis, was an adventive plant, collected at Port Juvénal, Montpellier, by Godron in 1852, when the native habitat of the species was unknown. The plant on which the later name, *B. amplexicaulis*, was based was stated by Cosson (Bull. Soc. Bot. Fr. 6: 613. 1859) to have been collected in Algeria by Durieu in 1844.

This very distinctive species is somewhat variable in size of the plant and its parts, especially the heads, florets, and achenes. There is some indication also of a tendency toward geographical differentiation in this species. It has been stated by Battandier (Bull. Soc. Bot. Fr. 59: 422. 1912) that his var. *decumbens* (cf. m.v. 1) occurs on the high plateaus of Algeria, whereas the form found in the Mitidja and in one part of the Chélif is erect and robust with shorter peduncles. From the limited specimens available to the present writer it is impossible to determine how definite this geographical segregation really is. It can be stated, however, that decumbent forms also occur in interior lowland districts, for example, near Gafsa, Tunisia. Again, certain specimens from Tunisia (collected near Tunis and Feriana) have flower heads, florets, and achenes at the lower limit of size. At the same time, a specimen collected near Sfax, in S. Tunisia, has the same parts near the upper limit of size. So the recognition of geographical segregates differing consistently in size characters can hardly be supported by the limited evidence now available. Future field studies, however, may reveal the existence of subspecies.

Eastern half of Algeria, Tunisia, and Tripolitania; adventive at Montpellier, France. Reported by Jahandiez and Maire (R. Cat. Pl. Maroc 3: 851. 1934) from E. Morocco at Taourirt; so it may occur in W. Algeria. Reported also from the S.W. Moroccan port of Safi, where it may be adventive.

The type, in Herb. Monspeliensis, was collected by Godron, in 1852, in Montpellier near Port Juvénal. A photograph of the type and fragments from the type collection are in Herb. Univ. Calif. (UC 296069); an isotype is in Herb. Ist. Bot. Univ. Firenze.

Algeria: S.W. Constantine, Oasis of Biskra, *Balansa* 778 (Ms, DL), as *B. amplexicaulis*, compared with type; Maison Carrée, *Battandier* 43 (DL), as *B. amplexicaulis*, compared with type; Biban, Portes de Fer, *Battandier and Trabut* 552 (P, UCf, Rome, as *C. senecioides*); *ibid.*, (UC ex Herb. Alger), as *C. amplexifolia* var. *decumbens* Batt. = m.v. 1; S.W. Constantine, near Biskra, El Outaya, *Battandier* (UC ex Herb. Alger) m.v. 1; Constantine, Djebel-Chattaba, prairie d'Aïoun-Seba, *Reboud* 2145 (K). **Tunisia:** Tunis, *Cosson et al.* in 1883 (PC); environs of Tunis,

Chabrolin in 1930 (UC); Sidi Tabet, near Tunis, *Chabrolin* in 1931 (UC); Zougag, near Kelibia, *Chabrolin* in 1932 (UC); Sbeitla, east of Feriana, *Chabrolin* in 1932 (UC); Bou Fichta, *Chabrolin* in 1935 (UC); S.W. Tunisia, Wadi Gafsa, *Eig* in 1931 (HU); Sfax *Pitard 611* (Mu). **Tripolitania**: Tripolis, *Krause* (B).

Minor Variant of C. amplexifolia

1. (*C. amplexifolia* var. *decumbens* Batt. in herb.) Typical of the species, except that the plants are often low and more or less decumbent. This habit, at least in some plants, may be genetically determined; but a tendency toward decumbent habit is found in collections from various localities. *Battandier* (UC ex Herb. Alger) El Outaya, near Biskra, S.W. Constantine.

Relationship

Crepis amplexifolia is intermediate between *C. aculeata* and *C. atheniensis* in degree of reduction in size of florets and achenes. The fruits are generally similar to those of *C. aculeata* but much more reduced.

186. *Crepis atheniensis* sp. nov.

(Fig. 290.)

Herba annua, circa 4.5 dm alta; radix tenua fibrosa in caudicem foliosum circa 1.5 cm latum abrupte delantanda; folia caudicalia interdum 12 cm longa 3 cm lata lanceolata acuta irregulariter runcinato-pinnatifida breve petiolata tenuiter pubescentia; folia caulina numerosa parva lanceolata acuminata sessilia acute auriculata; caules numerosi semi-decumbentes arcuate ascensi glabri remote 4-6-ramosi, ramis inferioribus elongatis, superioribus cymoso-corymbiformibus; pedunculi 1-7 cm longi glabri vel tomentosi; capitula erecta parva multiflora; involucri cylindrica in fructu 9-10 mm longa 5-6 mm lata, squamis exterioribus numerosis 0.5-0.8 mm latis lanceolatis acuminatis glabris stramineis ad apicem purpurinis, interioribus circa 13 lanceolatis acutis valde setosis, setis 1.5-2 mm longis flavis eglandulosis, in facie interiore dense pubescentibus ad maturitatem valde carinatis incurvatis et spongioso-incrassatis; receptaculum alveolatum ciliatum; corolla circa 11 mm longa, ligula circa 8 mm longa 1.25 mm lata flava in dorso rubescenti, tubo pubescenti pilis albis brevissimis; antherae 2.75 mm longae; rami styli circa 1.25 mm longi flavi; achaenia biformia, marginalia flavida 4.5 mm longa 0.5 mm lata ad apicem gradatim attenuata vel breve rostrata a latere compressa, interiora fusca 5.5-6.5 mm longa 0.4-0.5 mm lata tenuiter rostrata fusiformia 10-costata; pappus albus 4-5 mm longus 1-seriatus tenuissimus mollis barbellulatus caducus.

Annual, 4.5 dm high; root slender, fibrous, abruptly expanded into the leafy caudex; caudex 1.5 cm wide; caudical leaves up to 12 cm long, 3 cm wide, lanceolate, acute, irregularly runcinate-pinnatifid, the segments close, retrorse and denticulate, attenuate into a short winged petiole with broader base, finely pubescent with short pale glandless hairs; cauline leaves numerous, small, lanceolate, acuminate, sessile, subamplexicaul, acutely auriculate, denticulate or entire, sparsely pubescent or glabrous, uppermost bractlike; stems numerous, semidecumbent at base, arcuately ascending, terete, striate, glabrous, remotely 4-6-branched, lower branches elongated, cymosely 2-3-headed, upper branches cymose-corymbiform; peduncles 1-7 cm long, glabrous or tomentulose, slightly thickened near head; heads erect, rather small, many-flowered; involucre cylindric, 9-10 mm long, 5-6 mm wide in fruit; outer bracts 10-14 with 2-3 closely subtending, nearly equal in anthesis, $\frac{1}{3}$ - $\frac{1}{2}$ as long as inner bracts in fruiting heads, 0.5-0.8 mm wide, lanceolate, acuminate, stramineous, purplish at tip, glabrous, rounded-carinate before anthesis, becoming lax in fruit; inner bracts 12-14, lanceolate, acute, membranous at margin, with a median dorsal row of strong yellow glandless setae 1.5-2 mm long, becoming strongly carinate and incurved, enclosing marginal achenes, spongy-thickened at

base, densely pubescent on inner face with yellow shining hairs, not reflexed at maturity; receptacle aveolate, alveolae 0.4–0.5 mm wide, fimbriae low, membranous, very finely ciliate, cilia 0.1 mm long, white; corolla about 11 mm long; ligule about 1.25 mm wide; teeth 0.2–0.3 mm long; corolla tube 3–3.5 mm long, pubescent

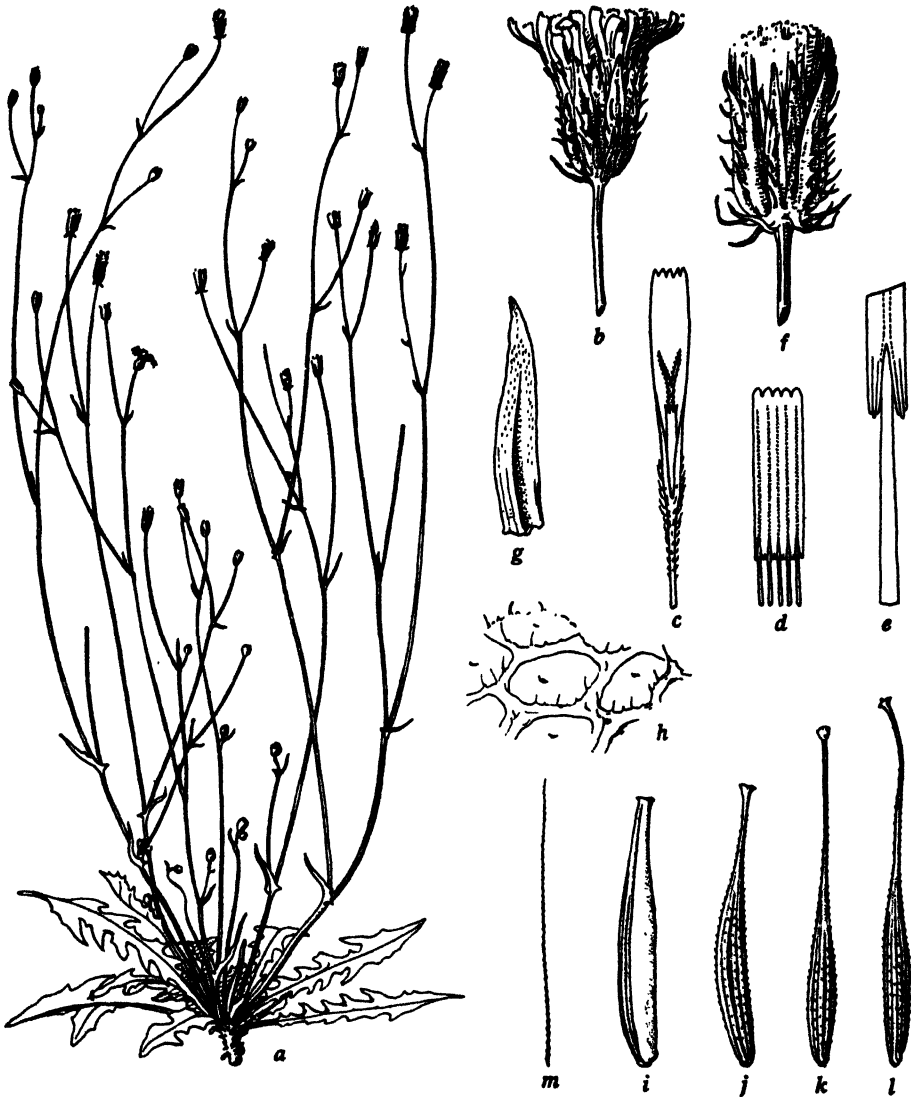


Fig. 290. *Crepis atheniensis*, from type (B): a, plant, $\times \frac{1}{4}$; b, flowering head, $\times 2$; c, floret lacking ovary, $\times 4$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, fruiting head, $\times 2$; g, inner involucre bract, inner face, $\times 4$; h, detail of receptacle, $\times 25$; i, j, marginal and, k, l, inner achenes, $\times 8$; m, pappus seta, $\times 8$.

with white acicular hairs up to 0.3 mm long, extending onto ligule; anther tube 2.7×0.8 mm dis.; appendages 0.3 mm long, lanceolate, acute; filaments 0.75 mm longer; style branches 1.25 mm long, 0.1 mm wide, yellow; achenes biform, marginal yellowish, 4.5 mm long, 0.5 mm wide, gradually attenuate upward or with a coarse beak about 1 mm long, laterally compressed, ventrally paler and striate or faintly ribbed, dorsally ribbed and spiculate, inner achenes tawny, 5.5–6.5 mm long,

0.4–0.5 mm wide, finely beaked, beak equal to or slightly longer than body, body fusiform, 10-ribbed, ribs rounded, strongly spiculate on upper half and somewhat thickened near the narrow oblique slightly calloused base, beak nearly smooth, 0.05–0.1 mm wide near summit, conically expanded into the 0.25 mm wide pappus disk; pappus white, 4–5 mm long, 1-seriate, very fine, soft, finely barbellulate, caducous. Flowering May–June; flowers yellow, ligules purplish on outer face.

Known only from the type locality.

Monomorphic.

Greece: Athens, in a place planted with olives "loc. pr. Hag. Anna," *Heldreich*, June 6, 1848, flowers and fruits, a single specimen (B, UCf) as "*Pterotheca nemausensis*, *cf. Rodigia*."

Relationship

C. atheniensis is related to *C. amplexifolia*, *C. aculeata*, and *C. aspera*, but it is very distinct, especially in the outer involucreal bracts, which are, like those in *C. foetida commutata*, numerous, narrow, and definitely carinate. But in no other respect does this species approach closely to *C. foetida*. To *C. amplexifolia* it shows considerable resemblance in floral characters and in the shape of the marginal achenes; but it is very different from that species in habit and leaf shape, in several involucreal characters, and in the strongly ribbed inner achenes and longer pappus. *C. atheniensis* is also distinct from *C. aculeata* and *C. aspera* in leaf shape, in floral characters, and in the marginal achenes. In size and shape of the fruiting heads, as well as in the long yellow setae on the inner involucreal bracts, this species approaches *C. aculeata*. In surface of the receptacle and size and shape of the inner achenes it resembles *C. aspera*. In habit it also resembles some forms of *C. aspera*. The possible identity of this species with *Endoptera intermedia* Boiss. (Diag. Pl. Or. Nov. ser. 2, 3: 99. 1856) has been considered. It seems more probable that Boissier's plants represent one of the variable races of *C. aspera* (cf. m.v. 3 of that species). The possibility that *C. atheniensis* originated through hybridization between *C. amplexifolia* and either *C. aculeata* or *C. aspera* may be noted, but the marginal achenes of *C. atheniensis* show no influence of either *C. aculeata* or *C. aspera*, both of which have highly distinctive marginal achenes, and in floral characters *C. atheniensis* is very different from those species. Furthermore, natural hybrids between the three species have not been reported in nature, although *C. aspera* has been crossed artificially with the other two and the hybrids are somewhat fertile. But none of those species is a native of Greece. Moreover, *C. amplexifolia* is widely separated geographically from the other two species. Hence a natural hybrid involving *C. amplexifolia* is practically out of the question. It seems remarkable that *C. atheniensis* has not been collected previously. The type specimen was very fruitful and would have produced hundreds of fertile achenes. It seems hardly possible that it could be a strictly local species, unless, being indigenous on some island, it may have been adventive in the vicinity of Athens.

187. *Crepis aspera* L., Sp. Pl. ed. 2, 1133. 1763.

(Fig. 291.)

Annual, 0.5–7 dm high; root vertical, very slender to robust; caudex 0.1–1 cm wide; caudical leaves few to numerous, (2) 6–12 (24) cm long, (0.5) 1–3 (5) cm wide, oblanceolate, obtuse or acute, denticulate, irregularly dentate or \pm pinnatifid with oblong or lanceolate dentate lateral lobes, glabrous or scabridulous, especially on margin, the teeth corneous-mucronate; lowest cauline leaves similar, the others gradually reduced toward summit of plant, oblanceolate, oblong or lanceolate, acute or obtuse, denticulate or coarsely dentate to pinnately parted with narrow

segments, sessile, usually amplexicaul and auriculate, the uppermost sometimes setulose; stem erect, simple, cymosely branched above, or remotely branched from near base upward, or divaricately much branched from the base and then sometimes decumbent or prostrate, stem, branches, and peduncles sparsely to densely beset with yellow or brown glandless setae or occasionally completely glabrous; peduncles up to 4 cm long, the first head in a cluster or sometimes 2 or 3 heads in a series nearly or quite sessile; heads small or medium, many-flowered; involucre turbinate when mature, 6–9 mm long, 4–7 mm wide, canescent-tomentulose; outer bracts 5–7, short, ovate or lanceolate, acute, membranous, glabrous; inner bracts 7–8, lanceolate, acute, pubescent within, \pm setose dorsally, becoming strongly navicular, enclosing marginal achenes; receptacle alveolate, fimbriellae densely ciliate; corolla 8–11 mm long; ligule 1.5–2 mm wide; teeth 0.1–0.75 mm long, the middle one much larger; corolla tube 2.5–3 mm long, pubescent with acicular hairs up to 0.3 mm long; anther tube (3)3.5 \times 1 mm dis.; appendages 0.4–0.65 mm long, oblong, acute; filaments 0.25 mm longer; style branches 1–2 mm long, 0.1 mm wide, yellow or green; achenes biform or uniform, when biform the marginal greenish or stramineous, 5–6 mm long, 1–1.5 mm wide dorsoventrally, strongly compressed, nearly straight or strongly curved or angled near base, gradually attenuate to the broad or narrow apex, dorsally convex, 3-alate, the ventral wing prominent, thin, and sometimes bearing a small claw near the apex, inner achenes (or all when uniform) tawny or pale brown, 5–7 mm long, finely beaked, the body 2.5–4 mm long, subterete, 10-ribbed, ribs narrow, pale, rounded, spiculate, beak pale, about 0.1 mm wide, smooth or striate, with expanded pappus disk; pappus white, 3–4 mm long, 1–2-seriate, fine or very fine, soft, deciduous. Flowering April–June; flowers yellow, ligules red on outer face. Chromosomes, $2n = 8$. The karyotype illustrated (fig. 286, n) has been found in 4 other accessions from widely separated localities.

Nemauchenes aculeata Cass., Dict. 34: 362. 1824–1825.

N. inermis Cass., *op. cit.*, 363.

Endoptera aspera DC., Prod. 7: 178. 1838.

Pterotheca aspera Rehb. f., Ic. Fl. Germ. Helv. 19: t. 77. 1858–1859.

Hieraciodes asperum O. Kuntze, Gen. 1: 345. 1891.

E. Mediterranean reg., from N. Syria to N.E. Egypt, from the coast to Aleppo, Anti-Liban, Transjordan, and N.W. Arabia; also in Cyprus; collected once in Iraq; reported from Crete but, acc. to Halaesky, not found there recently; said to occur in Libya, Italy, Thrace, and Hungary; presumably adventive in the last 5 places.

A definitely polymorphic species, which may be explained in part by the great diversity of habitats in which it is found. But our observations on various strains, in cultivation for several years under comparable conditions, indicate that many genetic variations also occur. There are, for example, wide differences in time of maturity and in habit (see m.v. 3); a number of strains lack completely the characteristic marginal achenes, and in one strain marginal achenes of an intermediate type occur (m.v. 3); the flower color may be pale or deep yellow and the style branches yellow or green; and there are striking differences in the character and amount of leaf dissection. At the same time the quantitative characters of the flowers and fruits seem to be fairly constant. Careful distributional studies combined with cultural tests might reveal the existence of well-marked geographic races or subspecies, although there is apt to be considerable variation in any locality, owing to the fact that the individual plant is highly self-sterile.

Orient: *Hasselquist* (L) type (photo UC). **Syria:** Aleppo, *Hohenacker* 177 (G, Mo); Gebel Druz, around Sueda, *Zohary* in 1931 (UC); Hama, *Zohary* in 1931 (UC); Anti-Liban, near Baal-

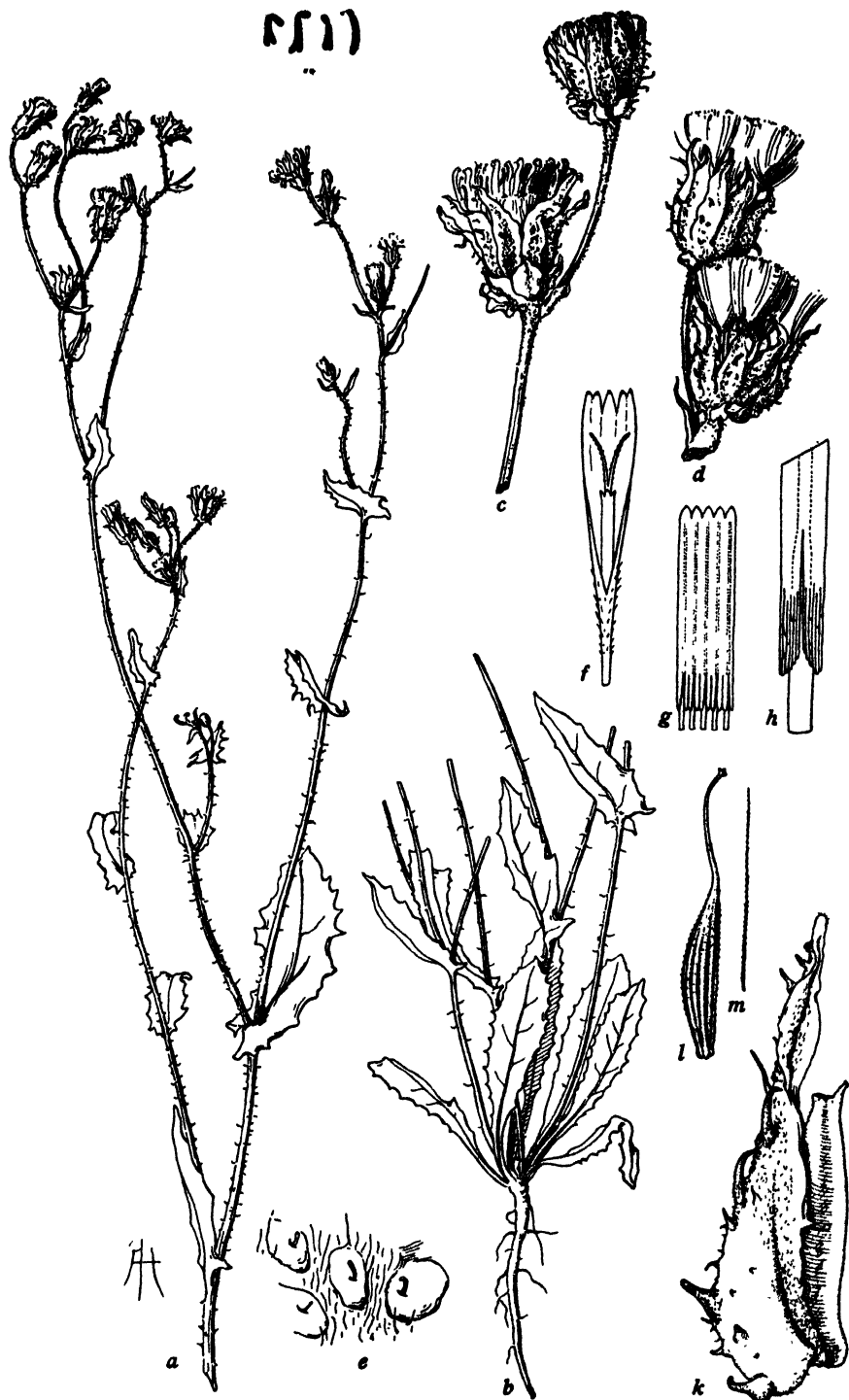


Fig. 291. *Crepis aspera*, a, from type (L); b-h, from hort. genet. Calif. 2500 (UC 446490); k-m, from type of *Endoptera aspera* (DC); n, from hort. genet. Calif. 1135 (grown from seeds received from Madrid Bot. Gard.): a, plant lacking root, $\times \frac{1}{2}$; b, lower part of plant, $\times \frac{1}{2}$; c, flowering heads, $\times 2$; d, fruiting heads, $\times 2$; e, detail of receptacle, $\times 25$; f, floret lacking ovary, $\times 4$; g, anther tube, $\times 8$; h, detail of appendages, $\times 32$; i, inner involucre bract enclosing marginal achene, $\times 8$; l, m, inner achene and a pappus seta, $\times 8$; n, somatic chromosomes, $n = 4$, $\times 1250$.

bek, *Bornmüller 18091* (Bornm.) m.v. 2; Tripoli, *Blanche* (G); Beirut, *Zohary* in 1931 (UC); Saïda, *Stauch* ? in 1853 (Bo) m.v. 1. Palestine: Gilead, *Medjdel*, *Eig* in 1927 (HU); Transjordan, *Es Salt*, *Eig* in 1929 (HU); Jericho, *Bornmüller 963* (B); Jordan Valley, *Ghor-es-Sufieh*, *Eig* in 1925 (HU, UC) m.v. 3; Jaffa, *Kneucker* in 1904 (G); Jerusalem, *Meyers and Dinmore* (G, Minn); *Raffa*, *Eig* in 1927 (HU, UC); between Beer-Sheba and Tel-Melah, *Eig* in 1927 (HU, UC); Moab, near El-Hasa, *Eig* in 1929 (HU, UC); Petra, *Deflers* in 1892 (Ms). Egypt: Ramlet-el-Echfen, *Ascherson 282* (B). Cyprus: near Yalussa, *Sintenis and Rigo 284* (B); without locality, *Deflers 757* (Ms).

Minor Variants of *C. aspera*

1. (*C. aspera* var. *inermis* [Cass.] Boiss., Fl. Orient. 3: 857. 1875.) "Stems and branches without setae; leaves glabrescent; inner bracts sparsely aculeate." Merely an extreme variant in amount of pubescence. Such variation in varying degree occurs commonly throughout most of the range of the species. *Stauch*? in 1853 (Bo) Bordu du Hamti, Saïda, Syria.

2. (*C. aspera* var. *dillacerata* Bornm., Fl. Lib. 237. 1914; Post, Fl. Syr. Pal. Sinai ed. 2, 2: 157. 1933.) "Leaves oftener divided to the rachis in sublinear lobes." In Bornmüller's type it is only the cauline leaves that are thus divided, and this is not infrequent in this species. It is hardly worthy of varietal rank. Photograph in Herb. UC. *Bornmüller 12091* (Bornm.), near Baalbek, Anti-Liban, Syria.

3. Extremely modified by adverse environment, possibly by saline soil. Plant diffusely branched from base, prostrate or decumbent, about 4 dm wide, tomentulose but almost devoid of the characteristic yellow setae, although a few occur on branches and involucre; caudical leaves absent; cauline leaves lanceolate, acute, pinnatifid, not amplexicaul; heads rather small; involucre 6–7 mm long; florets typical but at lower limit of size for the species; achenes all beaked, but some of the marginal ones gradually attenuate and obscurely angled. This plant was identified by the collector as "*Crepis arabica*," probably referring to *C. arabica* Boiss., which is *C. senecioides* Del., a very different species. Fortunately it was possible to grow some progeny from this plant for comparison with various strains of *C. aspera*. Although these offspring were extremely precocious, and in this respect resembled *C. senecioides* more than most races of *C. aspera*, yet in height of plant, and in leaves, heads, flowers, and fruits, they resembled other races of *C. aspera*. Some of them bore marginal achenes that are intermediate between the typical marginal and inner achenes of this species. But this tendency has been noted in other races. If the original plant were a hybrid between *C. senecioides* and *C. aspera*, it could hardly have been so highly fertile. Also, the achenes are not at all like those of *C. senecioides* and the progeny were uniform. The progeny, however, did have a more spreading habit than other races of *C. aspera* under cultivation, and this, together with the peculiar marginal achenes, may indicate the existence of a distinct race or subspecies. This also is indicated by the fact that an F₁ hybrid between this form and a strain typical of the species (acc. no. 1135 from the Madrid Botanic Garden) was very vigorous, reaching 7 dm in height. Further collections with field and garden studies may decide this question. Specimens of the first generation progeny of this plant are in Herb. Univ. Calif. It should also be noted that *Endoptera intermedia* Boiss. (Diag. Pl. Or. Nov. ser. 2, 3: 99. 1856), which, to my knowledge, has never been referred to a recognized genus, and the type of which has not been seen by me, may be just another race of *C. aspera* with intermediate marginal achenes, since the specimens cited by Boissier are from Beirut and Sidon. *Eig* in 1925 (HU, UC) Ghor-es-Sufieh, Jordan Valley, Palestine.

Relationship

Crepis aspera is closest to *C. aculeata*, from which it is easily distinguished by the broader membranous outer involucral bracts, the longer pubescence on the corolla tube, the ciliate receptacle, and especially by the very different marginal and inner achenes. It is less close to *C. juvenalis*. The geographic areas of *C. aspera* and *C. aculeata* overlap and some forms of *C. aspera* are fully as precocious as *C. aculeata*. Hence it might at first appear that the polymorphism of *C. aspera* is due to natural hybridization with *C. aculeata*. The two species have been crossed artificially and the F₁ hybrids are 30–50 per cent fertile. *C. aculeata*, however, is a relatively stable species. Also, there is no evidence for the existence in nature of hybrid swarms, composed of intermediate forms between the two species. It may be that they actually come into contact very seldom and that, when they do, *C. aspera* flowers later than *C. aculeata*. The atypical marginal achenes found in some races of *C. aspera* are intermediate between the typical marginal and inner achenes of

that species, not between *C. aspera* and *C. aculeata*. The polymorphism of *C. aspera* is evidently caused by combinations of genetic and environmental factors.

188. *Crépis setosa* Hall. f., Roem. Arch. Bot. 1(2) : 1. 1797.

(Figs. 292, 293.)

Annual, 0.8–8 dm high; root slender, tapering; caudex 0.1–1 cm wide; caudical leaves few or many, up to 30 cm long, 8 cm wide, oblanceolate, obtuse or acute, denticulate, dentate, runcinate-pinnatifid or pinnately parted, terminal segment large or sometimes small, lateral segments triangular to lanceolate, acute, \pm dentate, attenuate into a narrow or broadly winged petiole with broader base, finely hispid, hairs pale, glandless; cauline leaves mostly lanceolate, acuminate, dentate to deeply lacinate near base, amplexicaul-auriculate, auricles acuminate; stem erect, short and branched from near base, or elongated and remotely branched from base to summit, terete, fistulose, sulcate or striate, \pm hispid, branches long, spreading or strict, paniculately or cymosely branched, few-headed; peduncles slender, erect, \pm hispid or like involucre setose, setae yellow, glandless; heads small to medium, many-flowered; involucre cylindric-campanulate, somewhat turbinate in fruit; outer bracts 10–14, longest $\frac{1}{2}$ as long as inner bracts, linear, acuminate, carinate, lax; inner bracts 12–16, lanceolate, acuminate, becoming strongly carinate, spongy-thickened at base, ventrally pubescent, membranous-margined; receptacle areolate-fimbriate, areoles 0.4–0.5 mm wide, fimbriae low, membranous, shortly ciliate; corolla yellow, with or without red on outer face of ligule; style branches dark green or pale yellowish-green; achenes deep or pale tawny, inner ones 3–5 mm long, fusiform, terete, slender-beaked, beak long or short; pappus white, 1-seriate, fine, soft, deciduous.

S. Europe from E. Spain to Crimea (and, acc. to Ledebour, Velenovsky, and Hegi, to the Caucasus); Asia Minor; fields and waste places in lower altitudes. Hegi (1173) states that this species is indigenous probably only in S. Austria, but that it has been introduced widely throughout Europe and has become naturalized in some of the warmer regions. The discovery, however, of a distinct subspecies (see below) in N. Greece, together with intermediate forms in N.W. Thessaly and Epirus, and the frequent occurrence of the species from the Pyrenees eastward through the Balkan Pen. to Macedonia, all seem to point to a wider native habitat. Frequently introduced with seeds of grass and other crops not only throughout Europe but also in North and South America and New Zealand, often naturalized.

Although variable in size, habit, and leaf shape, as well as in size of heads and florets, depth of yellow color and amount of red in the ligules, and in length of beak on the achenes, this is such a well-marked species that very few forms have been named. All such forms appear to be merely variations in degree of hispidity or in leaf shape, except Markgraf's small-headed variety, which may belong to either of the two subspecies but is quite probably subsp. *Topaliana*.

Key to the Subspecies of Crépis setosa

- Achenes all similar, definitely beaked; plant and heads usually larger; style branches dark green 188, *a. typica*
 Achenes of 2 shapes; marginal achenes beakless, compressed; plant and heads smaller; style branches pale yellowish-green 188, *b. Topaliana*

188, *a. Crépis setosa typica* Babc., Univ. Calif. Publ. Bot. 19: 403. 1941. Plant 1.8–8 dm high; involucre 8–10 mm high, 4–8 mm wide; corolla 10–13 mm long; ligule 1–1.6 mm wide, pubescent below with short acicular hairs; ligule teeth 0.15–0.25 mm long; corolla tube 3.5–4.5 mm long, pubescent with acicular hairs 0.05–0.6 mm long;

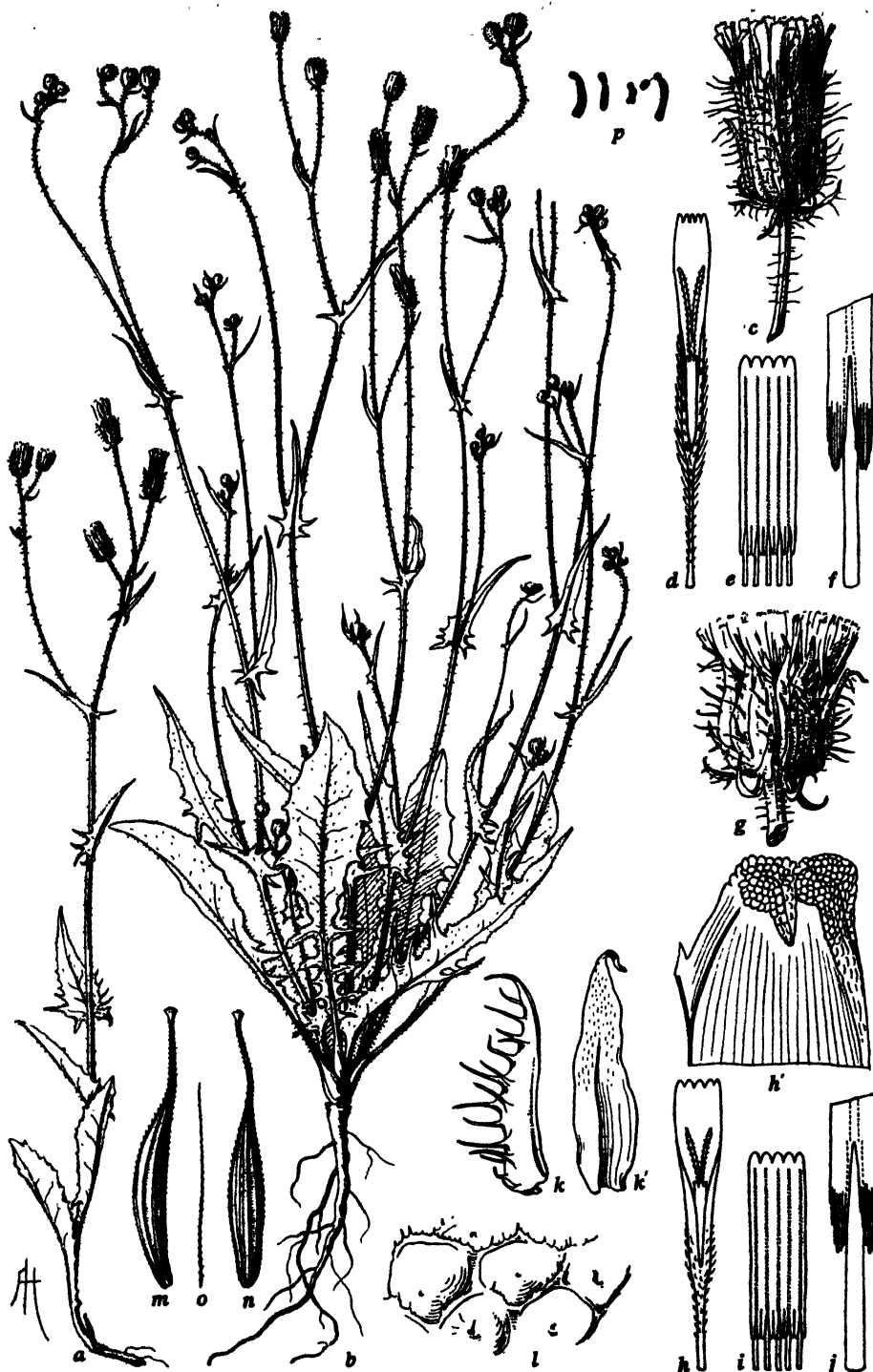


Fig. 292. *Crepis setosa typica*, a, from Kunisch in 1892 (UC 669435); b-f, from Lacaita in 1887 (BML 2933); g-o, from Georgieff in 1932 (UC 489402); p, from hort. genet. Calif. 1036 (grown from seeds received from Copenhagen Bot. Gard.): a, plant, $\times \frac{1}{4}$; b, plant, $\times \frac{1}{4}$; c, flowering head, $\times 2$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, fruiting head, $\times 2$; h, floret lacking ovary, $\times 4$; h', detail of ligule teeth, $\times 50$; i, anther tube, $\times 8$; j, detail of appendages, $\times 32$; k, k', inner involucre bracts, $\times 4$; l, detail of receptacle, $\times 25$; m-o, marginal and inner achenes and a pappus seta, $\times 8$; p, somatic chromosomes, $n = 4$, $\times 1250$.

anther tube 3.5×1 mm dis.; appendages 0.5 mm long, oblong, acute; filaments 0.5 mm longer; style branches 1.75–2.5 mm long, 0.1 mm wide, attenuate at tip, dark green; achenes deep tawny or pale brown, 3.25–5 mm long, 0.3–0.6 mm wide, fusiform, subterete, constricted at the calloused base, abruptly or gradually attenuate into a usually fine beak 1–2.5 mm long, with expanded pappus disk, 10-ribbed, ribs \pm prominent, narrow, rounded, strongly spiculate near base of beak; pappus 2.5–5 mm long. Flowering June–Nov.; flowers yellow with or without red on outer face of ligules. Chromosomes, $2n = 8$. See fig. 292.

Crepis setosa Hall. f., Roem. Arch. Bot. 1(2): 1. 1797.

C. hispida Waldst. et Kit., Pl. Hung. 1: 42. t. 13. 1802.

Barkhausia setosa DC., Fl. Fr. ed. 3, 4: 44. 1805.

C. bannatica Willd., Enum. H. Berol. Suppl. 55. 1813.

Wibelia setosa Röhl., Deutschl. Fl. 2: 258. 1826.

Hieraciodes setosum O. Kuntze, Gen. 1: 346. 1891.

C. glabrata Porcius, Anal. Acad. Romana ser. 2, 14: 157. 1892.

The type has not been seen by me; but the original description is full, detailed, and clear. The only inaccuracy concerns the achenes, and this was based on immature fruits, since Haller states: "Sed semina mihi negata fuerunt."

In addition to the critical and representative specimens cited below, numerous specimens covering the entire range of the species were available in Herb. Berol., and extensive collections from Italy are to be found in Naples, Rome, and Florence. Most of this material I have not studied critically; but many more specimens have been examined than are cited here, and several cultivated strains of both subspecies have been under observation and experimentation for a number of years.

Distribution of the species, except in N. Greece, where it is replaced by subsp. *Topaliana*.

Spain: Catalonia, San Hipolito de Voltrega, prairies, *Sennen 998* (UC); Andorra, 900 m, *Consturier* in 1913 (Mo); locality (?), *Lacaita* in 1887 (BML). **Italy:** W. of Taranto, Metaponto (Basilicata), fields, *Lacaita* in 1881 (BML). **Hungary:** *Kitaibel* (B in herb. Willd. no. 14747-1-4, p.p.); collector ? (B in herb. Willd. no. 14750-1-3) no. 3 = m.v. 1: central Hungary, *Dorner* in 1871 (Bur). **Austria:** *Richter 3416* (Bur). **Yugoslavia:** Dalmatia, near Cuttaro, *Pantocsek* in 1872 (Bur). **Greece:** Thessaly, above Kastanea, route to Zygos Mts., 300 m, *Babcock 351* (UC); below Kastanea, route to Kalabaka, *Babcock 348* (UC); Epirus reg., *Costopulos* in 1930 (UC) m.v. 3; Macedonia, Uskub dist., *Kisela-voda, Bornmüller 4214* (B); Macedonia, Roslog dist., *Bansko, Georgieff* in 1932 (UC); Macedonia, Koziani, S. base of Mt. Olympus, Ellasona, *Miss Topali* in 1937 (UC); E. Thessaly, northeast of Mt. Ossa, between Karitsa and Pyrgetos, *Miss Topali 38-7* (UC). **Bulgaria:** Sofia, *Stefanoff misit* in 1932 (UC). **Russia:** Crimea (Tauria) *Steven* in 1820 (DC Prod. vii: 155 no. 18-2). **Asia Minor:** Bithynia, between Moudamiah and Brusa (?), *Burnat* in 1889 (Bur); near Beykor, *Krause 4007* (UC) m.v. 2.

Minor Variants of *C. setosa typica*

1. Very robust; lower leaves up to 3 dm long, lanceolate, runcinate-pinnatifid, lateral segments triangular, acute, denticulate, and dentate, gradually attenuate to the broadly winged base; upper leaves typical; involucre 9 mm high; achenes about 4 mm long; pappus about 5 mm long. Herb. Willd. no. 14750-3. This plant, one of Willdenow's 3 specimens filed under *C. bannatica*, may be a garden hybrid with some other species, although the name shows that its origin was in S. Hungary.

2. Of low divaricate habit; stem short, branches slender; peduncles long, very slender, glabrous; heads small; florets short; style branches dark green; achenes all similar. Certainly a suppressed form, since garden plants from wild seed are normal in height and habit, although the heads are small for this subspecies. *Krause 4007* (UC) stony slope near Beykor, Bithynia, Asia Minor.

3. Stature and leaves more like those in subsp. *Topaliana*; peduncles setose; heads intermediate; corolla about 9 mm long, with little or no red on outer face of ligules; style branches 1.25 mm long, dark green; achenes biform, marginal ones more like those in subsp. *Topaliana*, although shortly beaked; pappus 4.5 mm long. Evidently an intergrading form between the two subspecies, perhaps of hybrid origin. Ex hort. genet. Calif. 31.3016a (UC) grown from wild seed collected by Wm. Costopulos in the Epirus reg., N.W. Greece.

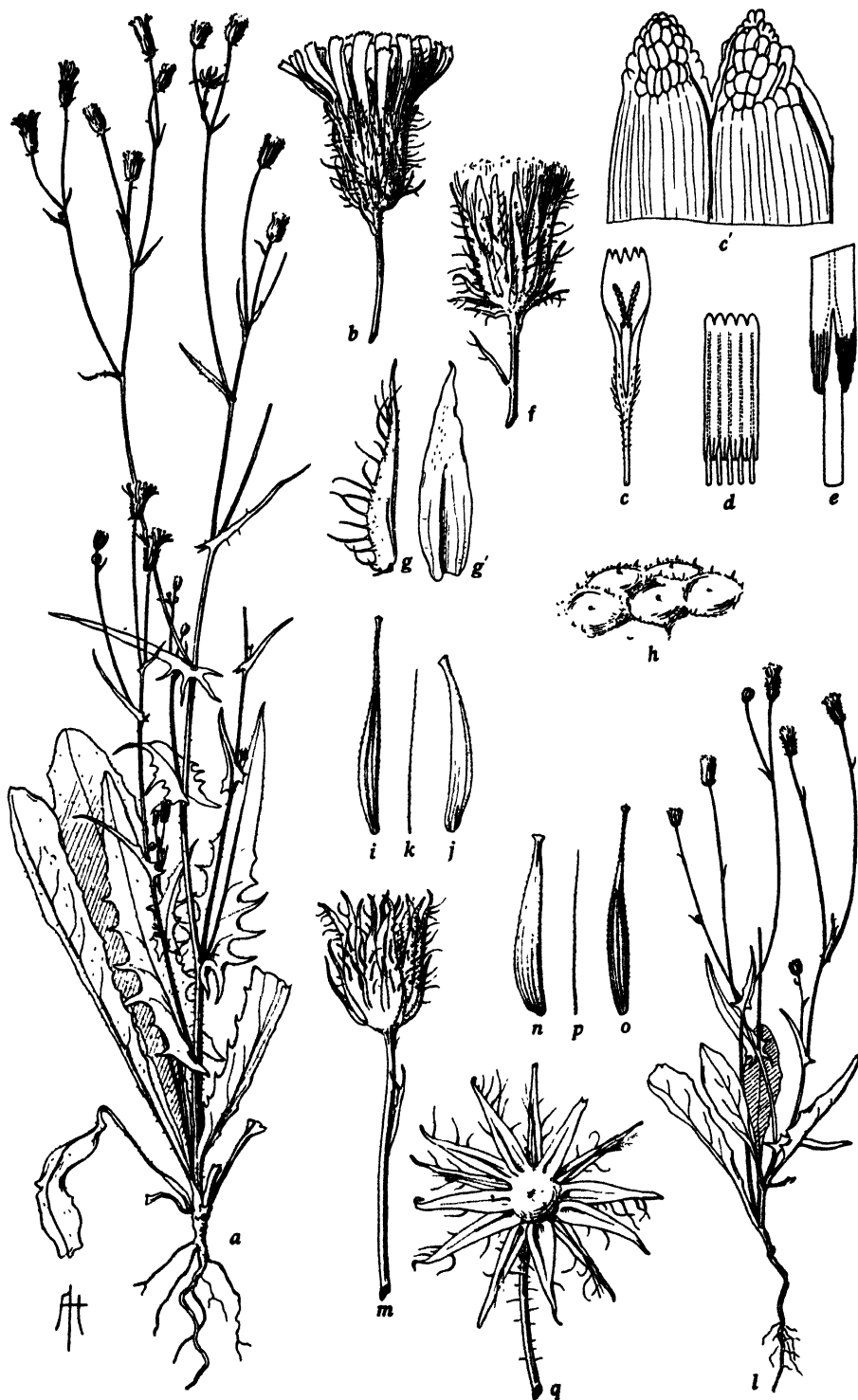


Fig. 293. *Crepis setosa* Topaliana, a-k, from type (UC 506855); l-q, from topotypes (UC 429357): a, plant, $\times \frac{1}{4}$; b, flowering head, $\times 2$; c, floret lacking ovary, $\times 4$; c', detail of ligule teeth, $\times 50$; d, anther tube, $\times 8$; e, detail of appendages, $\times 32$; f, fruiting head, $\times 2$; g, g', 2 inner bracts, $\times 4$; h, detail of receptacle, $\times 25$; i-k, 2 achenes and a pappus seta, $\times 8$; l, plant, $\times \frac{1}{4}$; m, old head, $\times 2$; n-p, 2 achenes and a pappus seta, $\times 8$; q, old head showing marginal achenes *in situ*, $\times 2$.

4. Very robust; heads relatively short and broad; achenes brown, 3 mm long, 0.6 mm wide, beak 1 mm long, less fine than in most forms; pappus 3 mm long. The short, relatively broad achenes with very short, coarser beak are found only on certain plants of a strain cultivated from seed collected in Oregon by Dr. C. V. Piper. Other plants of the same strain bear achenes 4–5 mm long, 0.5 mm wide, with beak slender, equal to body. Introduced, probably from Europe. Ex hort. genet. Calif. 30.1017–5 (UC) grown from seed collected at Silverton, Oregon, U. S. A.

188, *b. Crepis setosa Topaliana* Babco. Univ. Calif. Publ. Bot. 19: 403. 1941. Plant 0.8–3.5 dm high; involucre 7 mm long, 4–5 mm wide near base; corolla 8 mm long; ligule 1.75 mm wide, pubescent below with short acicular hairs; ligule teeth 0.15–0.5 mm long; corolla tube 3 mm long, pubescent with acicular hairs 0.05–0.4 mm long; anther tube 2.5×1 mm dis.; appendages 0.4 mm long, oblong, acute; filaments 0.4 mm longer; style branches 1.5 mm long, 0.1 mm wide, attenuate at tip, pale greenish-yellow; achenes bifiform, pale tawny or yellowish; marginal achenes 3 mm long, 0.5 mm wide, laterally compressed, ventrally straight with median ridge, paler, faintly ribbed, dorsally convex, darker, strongly ribbed, constricted at the rounded calloused base, gradually attenuate to the narrow summit, with slightly expanded pappus disk, not beaked or the beak less than 1 mm long, these sometimes absent or replaced by typical inner achenes; inner achenes 3–3.75 mm long, 0.3–0.4 mm wide, fusiform, subterete, constricted at the narrow calloused base, gradually or abruptly attenuate into a very slender beak 1–2 mm long, with abruptly expanded pappus disk, 10-ribbed, ribs narrow, rounded, strongly spiculate near base of beak; pappus 3–3.5 mm long. Flowering June–July; flowers yellow, with or without red on outer face of ligules. Chromosomes, $2n = 8$; the B-chromosome with distal arm shorter than in subsp. *typica*. See fig. 293.

Greece: Thessaly, Kato Lehonía, near Volo, *Miss Topali* in 1933 (UC) type; *ibid.*, grounds of Mr. P. S. Topali, *Babcock 338* (UC); *ibid.*, between Kato Lehonía and Drakia, *Babcock 360* (UC); Mt. Pelion, Portaria, *Miss Topali* in 1932 (UC); Thessaly, between Kalabaka and Kastanea, riverbanks and lower hills, *Babcock 346* (UC) m.v. 5; *ibid.*, along Penion R., above Kalabaka, *Babcock 356a* (UC) m.v. 6; Sporades Is., Skiathos, *Miss Topali* in 1932 (UC); E. Thessaly, north of Mt. Ossa, between Pyrgetos and Baba, *Miss Topali 38–10* (UC) near m.v. 5.

Minor Variants of *C. setosa Topaliana*

5. Style branches green; marginal achenes scarcely beaked, not laterally compressed, 2–2.5 mm long, ventrally flat, faintly ribbed; inner achenes 2.75–3.5 mm long, beak fine, 1–2 mm long; pappus 3 mm long. Probably a form derived from natural hybridization between the 2 subspecies. *Babcock 346* (UC), between Kalabaka and Kastanea, Thessaly, Greece.

6. Marginal achenes 3 mm long with beak 1 mm long, subterete or ventrally flat and paler; inner achenes 3.5 mm long, beak 1.5 mm long, very fine; pappus 3 mm long; style branches pale greenish-yellow. Probably only an extreme variant of this subspecies in the less modified, longer beaked marginal achenes. *Babcock 356a* (UC), along Penion R., above Kalabaka, Thessaly, Greece.

Relationship

Crepis setosa is closest to *C. Muhlisii*, from which it is well distinguished by the upright or ascending habit, longer oblanceolate lower leaves, and conspicuous cauline leaves; subsp. *typica* is also distinct in the uniform, longer, and usually longer-beaked achenes; and subsp. *Topaliana*, in the paler, longer-beaked inner achenes, the marginal achenes without basal scar, the broader corolla, and longer pale greenish-yellow style branches. *C. setosa* is less close to *C. aspera*, which it superficially resembles.

189. *Crepis Muhlisii* sp. nov.

(Fig. 294.)

Herba annua 0.7–1.5 dm alta; folia caudicalia 1–2.5 cm longa interdum 0.9 cm lata oblanceolata runcinata dentata vel denticulata in petiolum brevissimum attenuata pubescentia eglandulosa; folia caulina linearia sessilia auriculata parvis-

sima; caulis erectus tenuissimus glabrus 1-3-ramosus, ramis divaricatis 1-3-furcatis cum 2-4 capitula; pedunculi filiformes 1.5-5 cm longi tomentosi; capitula parva circa 50-flora virginea nutantia (?); involucrium in fructum 6-7 mm longum ad basim 3-4 mm latum, squamis exterioribus aequalibus interdum 2-plo brevioribus linearibus leviter carinatis, interioribus 12-14 lanceolatis acuminatis dense setulosis

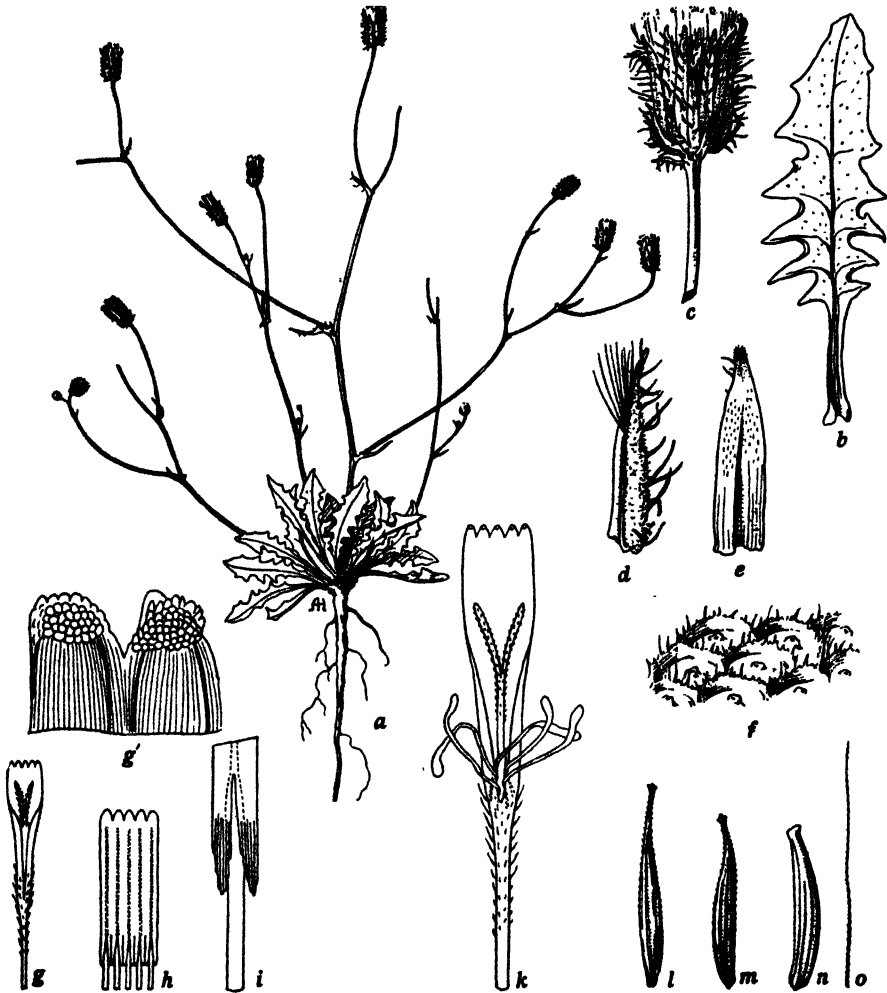


Fig. 294. *Crepis Muhlisii*, from type (UC 463868): a, plant, $\times \frac{1}{2}$; b, leaf, $\times 2$; c, fruiting head, $\times 2$; d, e, inner involucre bract, lateral view and inner face, $\times 4$; f, detail of receptacle, $\times 25$; g, floret lacking ovary, $\times 4$; g', detail of ligule teeth, $\times 50$; h, anther tube, $\times 8$; i, detail of appendages, $\times 32$; k, floret with abnormal anthers, $\times 8$; l-o, 3 achenes and a pappus seta, $\times 8$.

ventraliter pubescentibus in dorso valde carinatis achaenia marginalia includentibus; receptaculum alveolatum ciliatum; corolla 7.5 mm longa, ligula 1.25 mm lata flava in dorso purpurea, tubo 3 mm longo pubescenti; antherae normales 2.5 mm longae flavi; rami styli 1.25 mm longi virentes; achaenia fulva 2.5-3 mm longa biformia; marginalia a latere compressa pallida in dorso valde striata ad summum constricta vel breve rostrata valde spiculata; interioria fusiformia in rostrum tenue brevum gradatim attenuata 10-costata ad apicem valde spiculata; pappus albus 3-4 mm longus 2-seriatus tenuis mollis caducus.

Annual, 0.7–1.5 dm high; root slender; caudex up to 5 mm wide, leafy; basal leaves numerous, 1–2.5 cm long, up to 0.9 cm wide, oblanceolate, acute or obtuse, runcinately dentate or denticulate, attenuate into a very short winged petiole with broader base, pubescent on both sides with short pale spreading glandless hairs, apex and teeth corneous-mucronate; cauline leaves linear, sessile, entire or denticulate, acutely auriculate, very small, mostly bractlike; stem erect, very slender, terete, striate, glabrous, 1–3-branched from near base, branches widely divaricate, like axis 1–3-furcate, 2–4-headed; peduncles filiform, 1.5–5 cm long, \pm tomentose; heads nodding (?) before anthesis, small, about 50-flowered; involucre in fruiting heads 6–7 mm high, 3–4 mm wide near base; outer bracts 10–12, nearly equal, longest $\frac{1}{2}$ as long as inner bracts, linear, acuminate, pale below, dark near apex, shallow-carinate, glabrous or sparsely setulose; inner bracts 12–14, lanceolate, acuminate, canescent-tomentose below, dark near apex, densely beset with yellow glandless setules, appressed-pubescent on inner face, becoming strongly carinate, infolding marginal achenes; receptacle alveolate, alveolae 0.2 mm wide, fimbriae fleshy, shortly ciliate; corolla 7.5 mm long; ligule 1.25 mm wide, shortly pubescent near base; ligule teeth 0.15–0.2 mm long; corolla tube 3 mm long, pubescent with acicular hairs 0.05–0.3 mm long; anther tube (normal) 2.5×0.9 mm dis., often abnormal, anthers \pm degenerate, not united, partly fertile; appendages 0.5 mm long, lanceolate, acute or acuminate; filaments 0.4 mm longer; style branches 1.25 mm long, 0.1 mm wide, attenuate at apex, green; achenes (nearly mature) deep tawny, 2.5–3 mm long, biform; marginal achenes laterally compressed, ventrally straight, paler, obscurely ribbed, dorsally convex, strongly ribbed, with small oblique basal scar, strongly constricted below the expanded pappus disk or shortly beaked, strongly spiculate near summit, sometimes more like inner achenes in shape and ribs; inner achenes fusiform, subterete, constricted at the narrow calloused base, gradually attenuate into a fine beak about 1 mm long, 10-ribbed, ribs rather prominent, rounded, strongly spiculate near the apex; pappus white, 3–4 mm long, 2-seriate, fine, soft, caducous. Flowering May–June; flowers yellow, purple on outer face of ligules, ligule teeth deep purple.

Known only from the type locality.

Monomorphic.

Turkey (Bithynia): near Scutaria, Bulgurlu Dag, stony slope, about 150 m, *Krause 3210b* (UC 463868) type; *ibid.*, overgrown land, about 150 m, *Krause 3210* (UC).

Relationship

Crepis Muhlisii is closest to *C. setosa Topaliana*, from which it is easily distinguished by its darker, shortly beaked achenes, narrower florets with purplish ligules, shorter dark green style branches, low divaricate habit, and very small leaves. It is less close to *C. setosa typica*, from which it differs in the biform shortly beaked achenes, peculiar habit, and greatly reduced size throughout the whole plant. It is distinct from *C. fuliginosa* in the open divaricate habit, the few larger heads, the strong yellow setae on the involucre, the longer and narrower florets, and the larger more definitely biform achenes.

The very abnormal partly degenerate anthers, found in 4 of the 5 plants in Krause's original collections, are unique in *Crepis*, and this peculiar feature may be a dominant character. Numerous, normal-appearing pollen grains, however, were observed *before anthesis* in young florets from a plant exhibiting the abnormality uniformly after anthesis. In fully expanded florets the style branches have numerous pollen grains adhering to them, and other normal appearing grains were found on the abnormal anthers. These observations, particularly those made on florets

before anthesis, prove that the abnormal anthers are somewhat fertile and show that it might be possible for this retrogressive variation to be perpetuated by self-fertilization. The establishment in nature of such a radical departure from the typical morphology of the androecium would be a significant event in the current evolution of this genus. Additional collections and field observations are very desirable.

SECTION 27. PSAMMOSERIS

The 7 species comprising this most advanced section of the genus *Crepis* do not appear to be quite as homogeneous a group as those of the preceding section. But this is largely because the 4 more primitive members are perennials, whereas the other 3 are precocious annuals. The 4 perennials are adapted to montane or to

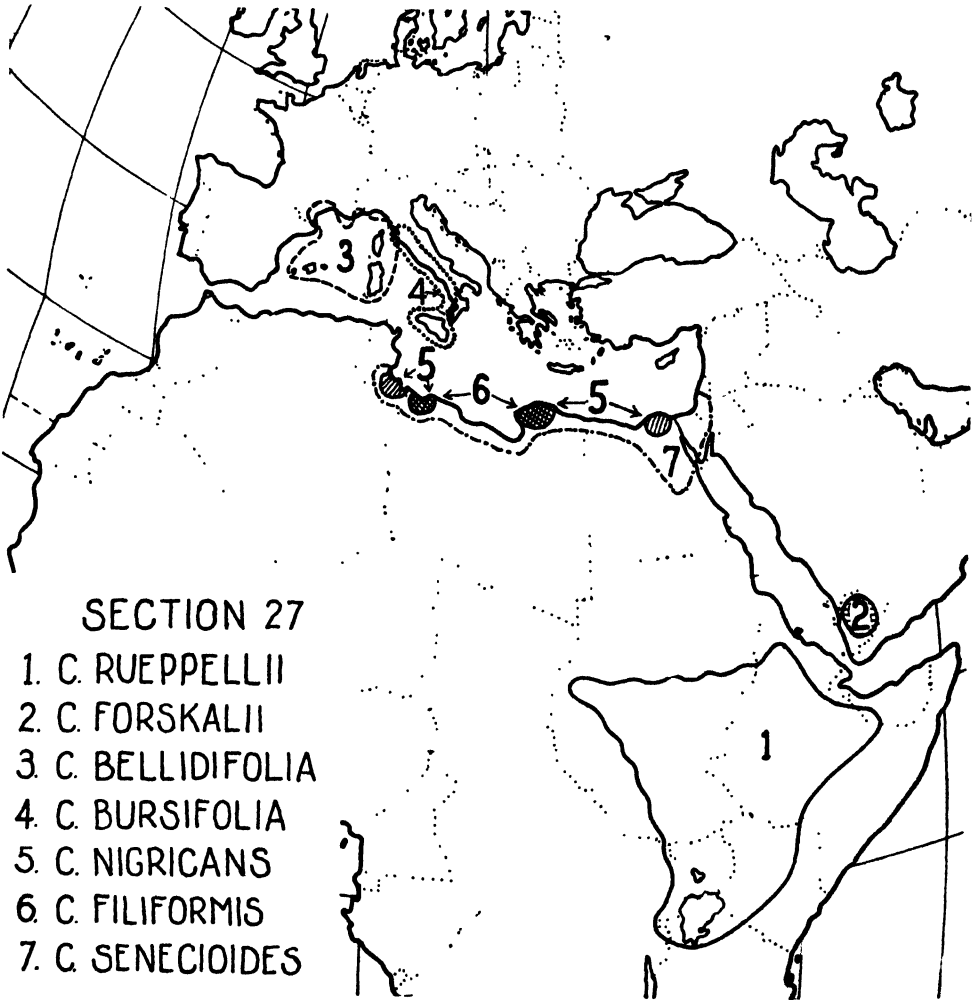


Fig. 295. Geographic distribution of the 7 species in sec. 27. The distribution of no. 7 is continuous from the Red Sea to Tunisia. Based on Goode *Base Map No. 201 PC*. By permission of the University of Chicago Press.

low maritime regions with more or less summer moisture. The others occur on the edges of oases and similar situations in the N. African-Mediterranean littoral. Thus, on the basis of length of life cycle and ecological relations, there are 2 distinct subgroups within the section. But morphologically all 7 species are closely similar except for differences in the roots and leaves. They are characterized by a leafy rosette from which arise several flexuous, nearly leafless stems bearing a few small flower heads. The involucre are very reduced, with a few short narrow outer bracts

and 8–14 inner bracts. The florets are mostly small, and the achenes are small, mostly with long slender or filamentous beaks bearing short white pappus setae which are fine or extremely fine, deciduous or caducous.

Subgroup A

The 4 perennial species consist of 2 pairs: (1) *C. Rueppellii* and *C. Forskalii*; (2) *C. bellidifolia* and *C. bursifolia*. The first two species are obviously closely related. They have a strong woody root, large denticulate or dentate basal leaves, and taller stems than any of the other species in the section. The involucre has only 8 inner bracts, but the florets and achenes are somewhat larger, at least in *C. Rueppellii*, than in all the other species. Unfortunately, it has not been possible to cultivate either of these two species, so their karyotypes cannot be compared. Very probably, as in the other species of this section, they have 4 pairs of choromosomes. Their geographic distribution is consistent with the morphological evidence of their close relationship, since *C. Rueppellii* occurs in Eritrea, Abyssinia, and adjacent regions, and *C. Forskalii* is restricted to Yemen Prov. in S.W. Arabia directly across the Red Sea from Eritrea (cf. fig. 295). The distribution of the most primitive species of this section in tropical Africa, and of its closest relative in adjacent Arabia, has definite significance in connection with the origin and migrations of the genus as a whole (cf. Part I, chap. 8).

C. bellidifolia and *C. bursifolia*, the other two perennial species, have very similar karyotypes and they are similar with respect to size and habit of the plant; but in almost every other detail they differ strikingly, most notably in the color and dissection of the basal leaves, the color of the outer face of the florets which is red in *C. bellidifolia* and greenish in *C. bursifolia*, and in the achenes which have a slender beak equal to the body in the former and a much longer filamentous beak in the latter. These two species are distributed in different littoral areas of the W. Mediterranean region (fig. 295). It seems very probable that *C. bellidifolia* originated in Corsica, where it is abundant throughout the island, and that it was distributed by man to its other locations; whereas *C. bursifolia* may have originated in Sicily, the home of several other *Crepis* endemics, and spread to the Italian mainland. At any rate, like the other two perennial species of this section, they are now distributed farther from the assumed center of origin of the genus in Central Asia than the three most advanced species of the section, a relationship which is found in several other sections of this genus (cf. Part I, chap. 5).

Subgroup B

The 3 precocious desert annuals, *C. nigricans*, *C. fliformis*, and *C. senecioides*, although generally similar, are very distinct in many details of their morphology (cf. figs. 302–304). Their distributional areas overlap (fig. 295), but there are no records of their occurrence at the same localities. However, even if they do occur together and are able to hybridize naturally, it is very probable that such hybrids would be less vigorous, or at least less fertile, than the parents; and under the rigorous conditions of their environment, this would certainly tend to preserve the three species.

Key to the Species of Section 27

Plant perennial, the root woody and recalcrescent; florets 9–13 mm long.

Basal leaves denticulate or dentate; involucre with 8–10 inner bracts, these with either black glandless or glandular setules on the outer face.

Longest outer involucral bracts $\frac{1}{2}$ as long as the inner ones; achenes 10–15-ribbed, attenuate in a definite but rather coarse and sometimes short beak; pappus 4.5–6 mm long, 2-seriate.....190. *C. Rueppellii*, p. 892

Longest outer involucral bracts $\frac{1}{4}$ as long as the inner ones; achenes 10-striate, abruptly constricted into a filiform beak equal to the body of the achene; pappus 3–4 mm long, 1-seriate.....191. *C. Forskalii*, p. 898

Basal leaves pinnatifid; involucre with 9–13 inner bracts, these either with or without yellowish setules on the outer face.

Involucre glabrous, tomentulose or gland-pubescent; ligules reddish-purple on outer face; style branches yellow; achenes with a beak $\frac{1}{4}$ – $\frac{1}{2}$ as long as the whole fruit.....192. *C. bellidifolia*, p. 900

Involucre setulose with yellowish glandless setules; ligules greenish- or bluish-gray on outer face; style branches green; achenes with a beak $\frac{2}{3}$ as long as the whole fruit.....193. *C. bursifolia*, p. 904

Plant annual, the root slender and ephemeral; florets 5–8 mm long.

Inner involucral bracts 12–14; longest outer bracts $\frac{1}{2}$ as long as the inner; achenes with a beak never more than $\frac{1}{2}$ as long as the whole fruit.

Stems branched, 3–9-headed; involucre about 3 mm wide in fruiting heads; achenes bifiform, the marginal shorter, shortly beaked, and more strongly ribbed; pappus 3 mm long.....194. *C. nigricans*, p. 906

Stems mostly 1-headed; involucre about 6 mm wide in fruiting heads; achenes uniform, with a beak about $\frac{1}{2}$ as long as the whole fruit; pappus 4 mm long.....195. *C. filiformis*, p. 908

Inner involucral bracts 8; longest outer bracts $\frac{1}{4}$ as long as the inner; achenes with a very delicate beak $\frac{3}{4}$ – $\frac{1}{2}$ as long as the whole fruit.....196. *C. senecioides*, p. 910

190. *Crepis Rueppellii* Sch. Bip.

Flora, 22: 20. 1839. (Pl. 36. Figs. 296–298.)

Perennial, 0.5–4.5 dm high; caudex vertical, woody, 0.5–2 cm wide, prolonged into a strong woody root, simple or \pm divided, leafy at crown; caudical leaves 3–18 cm long, 0.8–2.5 cm wide, oblanceolate, obtuse or acute, finely denticulate to irregularly deltoid-dentate, gradually attenuate into a winged petiole, canescent-tomentulose and pubescent with very short fine gland hairs or glabrous; lowest cauline leaves lanceolate or linear, acuminate, the others mostly bractlike; stems 1–4 or more, arcuate or erect, terete, striate, puberulous or glabrous, remotely branched usually from near base, branches pedunculate or cymosely 2–5-headed; peduncles 1–18 cm long, slender, 1–3-bracteate, puberulous or tomentulose; heads erect, medium or rather small, 25–40-flowered; involucre cylindric-campanulate, 8–11 mm long, 3–4 mm wide in fruiting heads before becoming lax; outer bracts 5–10, unequal, longest $\frac{1}{2}$ as long as inner bracts and 0.5–1 mm wide at base, lanceolate, acute, tomentulose or glabrous, with a dark median dorsal line or band; inner bracts 8, lanceolate, oblong-acute, rounded and white-ciliate at apex, dark in mid-region, membranous-margined, tomentulose, usually gland-pubescent and with a median row of short black setae sometimes bearing glands, ventrally pubescent with small white hairs or rarely glabrous, becoming \pm carinate and spongy-thickened at base at maturity, ultimately reflexed; receptacle alveolate, fimbriae low, fringed with short fine cilia; corolla 10–13 mm long; ligule 1.5–1.8 mm wide; teeth

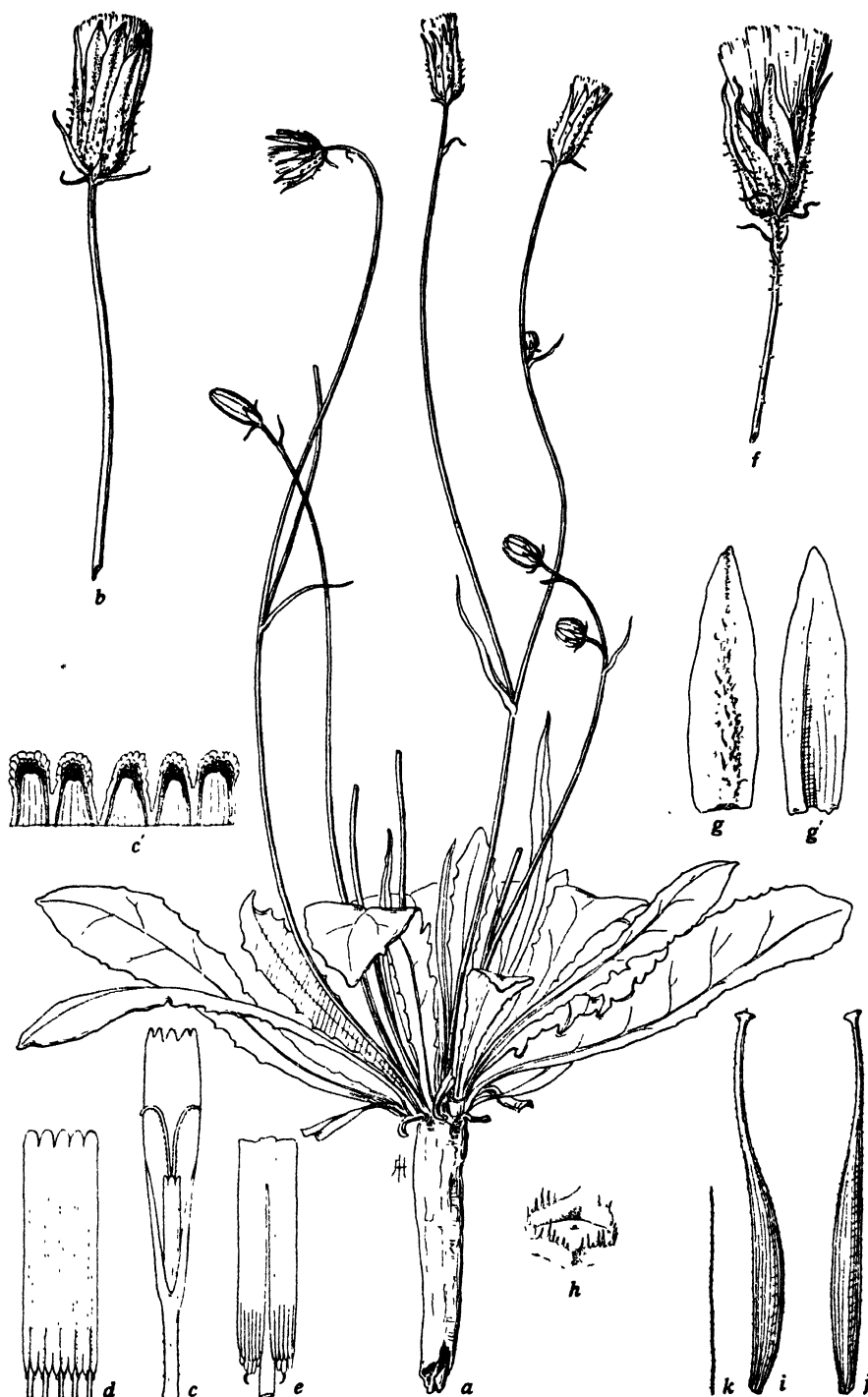


Fig. 296. *Crepis Rueppellii*, a-e, from Schimper 254 (on same sheet with the following); f-k, from an authentic spec. of *Rueppell* (PC): a, plant $\times 1$; b, immature head, $\times 2$; c, floret lacking ovary, $\times 4$; d, detail of ligule teeth, $\times 25$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, mature head, $\times 2$; g', inner involucre bract, outer and inner faces, $\times 4$; h, detail of receptacle, $\times 25$; i-k, 2 achenes and a pappus seta, $\times 8$.

unequal, marginal ones shorter, 0.2–0.4 mm long; corolla tube 3–4 mm long, \pm scabrous with very short papilliform hairs; anther tube (3.5)4.5 \times 1(1.2) mm dis.; appendages 0.8 mm long, oblong, obtuse, sometimes tipped with a minute claw; filaments short; style branches 1.75–2.25 mm long, 0.1 mm wide, yellow; achenes pale brown, tawny or stramineous, 5–6.5 mm long, about 0.5 mm wide, subterete, fusiform, gradually attenuate into a definite though sometimes very short and coarse beak, with expanded pappus disk 0.3 mm wide, constricted at the small calloused base, 10–15-ribbed, ribs nearly equal, narrow, finely spiculate to the apex; pappus white, 4.5–6 mm long, 2-seriate, setae nearly equal, fine, soft, deciduous. Flowering Jan.–Sept.; flowers yellow, reddish-purple on outer face of ligules.

Barkhausia adenothrix Sch. Bip., ex Richard, Fl. Abyss. 1: 465. 1847.

Brachydecea Rueppellii Sch. Bip., ex Schweinfurth, Fl. Aethiop. 1: 283. 1867.

Hieraciodes abyssinicum O. Kuntze, Gen. 1: 345. 1891.

The type, in Herb. Univ. Frankfurt, has flowers but no fruits; it is illustrated by Fries (Svensk Bot. Tidskr. 22: pl. V, f. 3). An authentic specimen of Schultz Bipontinus, collected by Rueppell, is in the Cosson herb., Paris; it consists of 2 flower stems with fruits but no flowers. These correspond with the type, so far as it is possible to compare them. Photographs of Schimper's specimens, named by Schultz Bipontinus, in herb. Cosson, Paris, are in Herb. Univ. Calif.

N.E. Africa in Eritrea, Abyssinia, British Somaliland, Kenya, Uganda, and W. Sudan, from 1600 to 2900 m alt.

Although rather variable in size of the plants and in length of the leaves and stems, this species is not actually as variable as Fries' treatment of the species implies, since his type of var. *centrali-africana* (Fries 1507) has been found to be a different species (cf. *C. Friesii*), and one of the other three specimens cited by Fries under that variety (*Mildbraed 1276*) is still another species (cf. *C. Mildbraedii*). At the same time, several notably divergent types have been found among the specimens seen by the present author, and it is possible that some of these will eventually be found to represent major subspecific entities. At present, however, the material is either so scanty or the divergencies from the range of forms which are accepted by Fries as typical are so trivial that, in the opinion of the present author, they should all be treated as minor variants.

Eritrea: Saganeiti, 2200 m, *Schweinfurth 1376* (B); *ibid.*, Gorge Gorja, near Addingofon, 2200 m, *Schweinfurth et Riva 879* (US); *ibid.*, Achele-Guzai, 2200 m, *Fiori 1895* (Fl, UCf); Hamasen, Az Teklezan (and Uara †), 2200 m, *Fiori 1893* (Fl, UCf). **Abyssinia:** *Rueppell* (Frankfurt type, PC authentic, ex herb. Sch. Bip.); near Adoa (= Adua), dry hills, *Schimper 217* in 1838 (PC, DL, B, Stockholm, UCf), as *C. (Barkhausia) adenothrix* Sch. Bip., msept.; near Adoa, *Schimper 217* (G), as *C. (Barkhausia) adenothrix* = m.v. 1; without locality, *Schimper 254* in 1854 (PC on same sheet with an original specimen of Rueppell); *ibid.*, *Schimper* in 1853 (B); Debra Tabor (Samara), *Schimper* in 1863 (B); *ibid.*, *Steudner 431a* (B); Gebel Gerara, 2560 m, *Rohlf's and Stecker* in 1880; "alto plano Talanta," *Rohlf's 29* (B); Galla highland, Uba, 2750 m, *Neuman 145* (B); Galla, Arussi, 2500 m, *Ellenbeck 1311* (B) m.v. 3. **British Somaliland:** Gebel Sérrut, Meid, 1700 m, *Hildebrandt 1439* (B) m.v. 2. **Kenya:** N. side of Mt. Kenya, between Liki and Kongoni R., *Themeda* grass association, *Fries 1521* (Uppsala); W. side of Mt. Kenya, Coles mill, 2000 m, *Fries 974* (Uppsala); W. Kenya, Nanyuki Forest Station, 2121 m, *Napier 2184* (K); Nandi, east of Lake Victoria, grass plains, 2121–2424 m, *Scott Elliot 6937* (K, B) m.v. 4. **Uganda:** Mt. Elgon, 1515 m, *Dummer 3717* (K) m.v. 6; Ruwenzori, *Scott Elliot 7595* (K, B) m.v. 5; N. Prov., W. Nile dist., Arua, 1535 m, grassland among scattered trees, *Greenway and Eggeling 7210* (UC, Amani) m.v. 8. **Uganda-Sudan Boundary:** S.E. Imatonga, Mt. Lomwaga, 2532 m, burnt grassland among trees and open bush on a gentle slope, *Greenway and Hummel 7273* (UC, Amani) m.v. 7. **Sudan:** Darfur, Jebel Marra, 2900 m, *Lynes 55* (K, US); *ibid.*, Niurnya, 2000 m, *Lynes 19* (K *ide* Fries).

Minor Variants of *C. Rueppellii*

1. (*C. Rueppellii* f. *megapoda* Babco., in herb.) Caudex nearly 2 cm in diameter and branched at summit, forming numerous small rosettes in a mat nearly 10 cm wide; caudical leaves only 2–4 cm long, 0.5–0.75 cm wide, denticulate to runcinate-pinnatifid, fuscous-tomentose on both sides and, like stems peduncles and involucre, sparsely pubescent with white hairs bearing brown glands; stems 15 cm high, 1–2-branched, branches arcuately spreading, 1–2-headed; peduncles 1–10 cm long; involucre 8–9 mm long, 5 mm wide at base; outer bracts 8, unequal, longest $\frac{1}{2}$ as long as

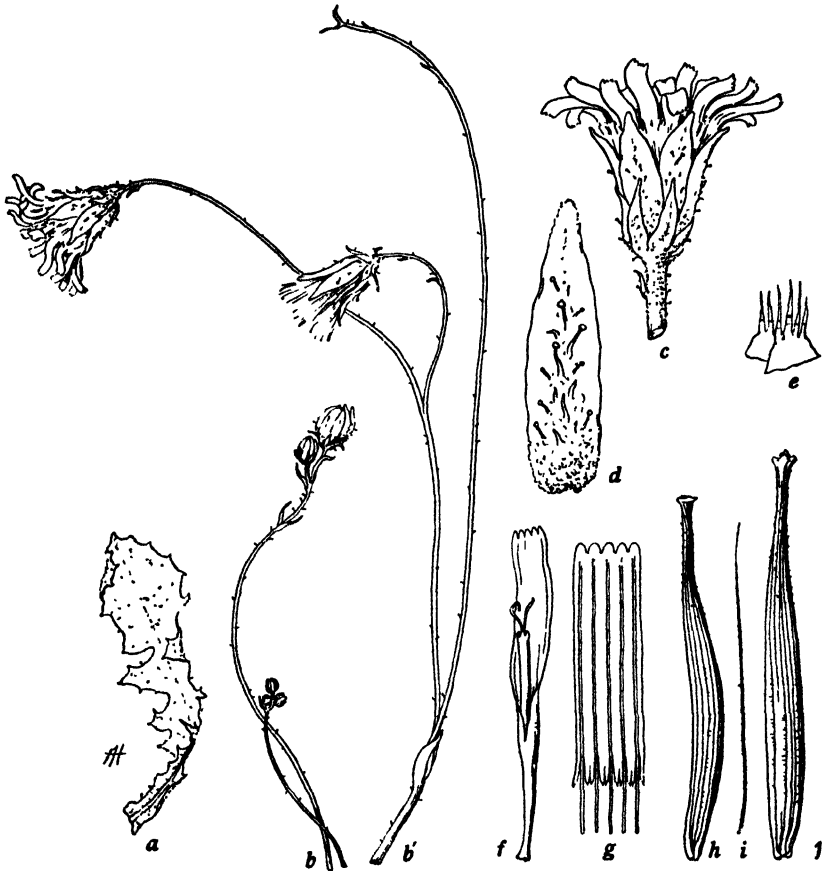


Fig. 297. *Crepis Rueppellii*, m.v. 1, from Schimper 217 (G, as *Crepis* [*Barkhausia*] *adenothrix* Sch. Bip., det. Hochst.): a, caudical leaf, $\times 1$; b, b', flower stems, $\times 1$; c, head, $\times 2$; d, inner involucre bract, outer face, $\times 4$; e, detail of fimbriae on receptacle, $\times 32$; f, floret lacking ovary, $\times 4$; g, anther tube, $\times 8$; h, i, j, marginal and inner achenes and a pappus seta, $\times 8$. Cf. pl. 36.

inner bracts and 1 mm wide at base; inner bracts 8, oblong-acute, rounded at tip, gland-pubescent and setose, setae glandular or glandless, tomentose, glabrous on inner face, becoming carinately thickened at base; receptacle fimbriate-ciliate; corolla 10.5 mm long; ligule 1.25 mm wide; corolla tube 3.75 mm long, glabrous; anther tube about 4×1 mm dia.; appendages 0.5 mm long, obliquely acute, tipped with a small claw; achenes dark brown, 5–7 mm long, 0.5–0.6 mm wide, fusiform, attenuate into a very short coarse beak, 12-ribbed, ribs rather strong and prominent at base, rugulose below, spiculate toward summit; pappus white, 5 mm long, soft. Known only from one specimen in Gray Herb. This specimen, from the Compositae of F. W. Klatt, is mounted on a sheet labeled "Schimper pl. Abyssinice. Ed. Hohenacker. 217. *Crepis* (*Barkhausia*) *adenothrix* C. H. Schultz Bip.—Hochst. Pr. Adoam" (cf. pl. 36). But this plant differs from the specimens of *C. Rueppellii* which were distributed as "n. 217. *C. (Barkhausia) adenothrix* C. H. Schultz Bip. (mscpt.) in Schimper's iter Abyss. Sectio prima: pl. Adoense." The chief distinguishing features of

this form follow: Caudex crassus, multiramosus; folia caudicalia numerosa, parva, pinnatifida, fusco-tomentosa; squamae involucri interiores interne glabrae; corolla glabra; achaenia nigrofusca, in rostro crasso et brevi attenuata. The outer involucrel bracts are very broad (see fig. 297, c) in contrast to those of some specimens of the species (see fig. 296, b, f); but these two figures represent the extremes which are connected by a continuous range among otherwise normal plants. In other respects there is general resemblance to *C. Rueppellii*; but future collections in the vicinity of Adua may reveal the existence of a distinct entity which must be recognized as a subspecies or species. Although this plant resembles *C. abyssinica* in its thick root and small leaves, yet it differs from that species in many ways, most notably in the inner involucrel bracts being glabrous within, in the fine cilia of the receptacle, the much larger florets with longer anthers, and especially in the achenes which are much larger and of different shape with more numerous ribs. From *C. xylorrhiza* this plant is equally distinct in its smaller glabrous corolla but larger anther tube; also in the narrower achenes, ciliate receptacle, and pubescence of the involucre. In both flowers and fruits this plant is certainly nearest to *C. Rueppellii*.

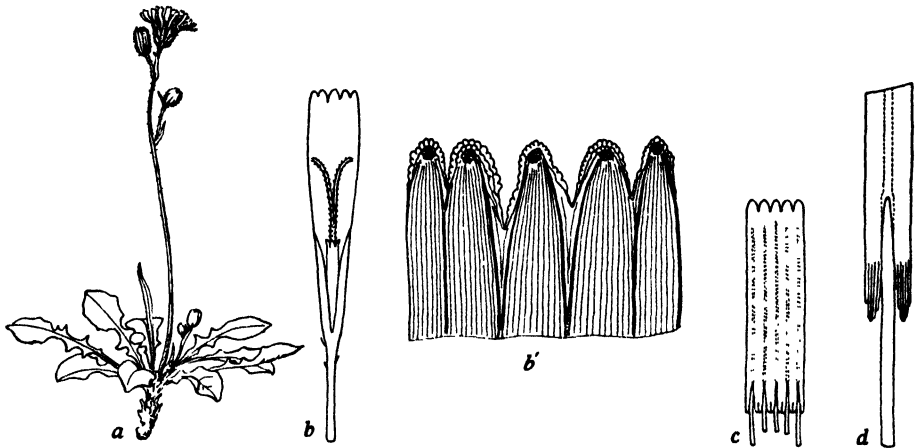


Fig. 298. *Crepis Rueppellii* var. *somalensis* R. E. Fr., from type (B): a, plant, $\times \frac{1}{2}$; b, floret lacking ovary, $\times 4$; b', detail of ligule teeth, $\times 50$; c, anther tube, $\times 8$; d, detail of appendages, $\times 32$.

2. (*C. Rueppellii* var. *somalensis* R. E. Fr., Svensk Bot. Tidsk. 22: 365. 1928.) Plant about 10 cm high; caudex 5 mm wide; caudical leaves numerous, up to 4 cm long, 1 cm wide, oblanceolate, lyrate pinnately parted, terminal lobe elliptic, apiculate, lateral lobes 2-4, triangular or rounded, denticulate, gland-pubescent with very fine and much coarser setiform pale hairs; stem and flower heads typical of the species; corolla 11-12 mm long; ligule 1.6 mm wide; teeth 0.15-0.4 mm long, very unequal, the marginal reduced; corolla tube 3.5 mm long, glabrous except for a few stout 1-2-celled hairs up to 0.25 mm long near summit; anther tube 3.5×1 mm dis.; appendages 0.5 mm long, narrow, oblong, acute, united, without a claw at tip; filaments 0.25-0.5 mm longer; style branches 2-2.25 mm long, 0.1+ mm wide, acute, yellow; achenes lacking; pappus white, about 5 mm long. Known only from the type specimen: *Hildebrandt 1439* (B) Meid, 1700 m, mountain reg. of Sérrut, British Somaliland. As suggested by Fries, this plant may represent a distinct subspecies or species, but owing to the scanty material, without fruits, and the general similarity of the inflorescence to that of typical *C. Rueppellii*, its present treatment as a minor variant seems warranted. Its chief distinguishing features are: the pinnately parted leaves and their setiform gland hairs; the nearly glabrous corolla tube which nevertheless bears a few trichomes unlike those found in plants typical of *C. Rueppellii*; and the short narrow anther appendages which lack a claw at the tip. (Fig. 298.)

3. Stems very numerous and robust; heads numerous and somewhat larger than in typical plants; involucre 10-13 mm high, 7 mm wide at base in fruit; largest outer bracts 1.5 mm wide; inner bracts becoming strongly carinate and conspicuously spongy-thickened at base; florets numerous; corolla 10-12 mm long; anther tube about 3.5 mm long; achenes mostly sterile. Since the pollen grains are 3-pored but somewhat irregular in shape and $22-34\mu$ in diameter, and the achenes are mostly sterile, it seems probable that this is a triploid form. Although such forms with aberrant chromosome numbers may be extremely rare, yet their potential role in the origin of either fertile or apomictic polyploid races should be remembered by collectors in the future. *Ellenbeck 1311* (B) in tall grass, mountain side, 2500 m, Arussi, Galla, S. Abyssinia.

4. Stems robust, sinuately erect, with strictly erect branches; inner involucrel bracts 8-12. This

unusual variation in the number of inner involueral bracts was noted by Fries, and the present author agrees that little importance need be attached to it, because only one head has as many as 12 inner bracts and the flowers and fruits appear to be typical. Of greater interest is the apparent tendency for the plant to have a more strict habit, since in this respect this variant is an intergrade toward the next two. *Scott Elliot 6937* (K, B) grass plains, east of Lake Victoria, 2121–2424 m, Nandi, W. Kenya.

5. Stems 2–4, erect, robust, 3.5–5 dm high, with strictly erect branches; outer involueral bracts $\frac{1}{4}$ – $\frac{1}{2}$ as long as inner bracts and 0.3–0.5 mm wide. To show the close correspondence with typical forms and a few minor differences, the following data are given: Involucre 8 mm long, 4 mm wide at base in fruit; corolla 12 mm long; ligule 1.5 mm wide; teeth 0.15–0.3 mm long; corolla tube 4.5 mm long, beset with stalked papilliform hairs up to 0.13 mm long; anther tube about 3.5×1 mm dis.; appendages 0.6 mm long, oblong, acute, without a claw at tip; filaments 0.75 mm longer; style branches 2.25–2.5 mm long, 0.15 mm wide, attenuate, yellow. *Scott Elliot 7595* (K, B) 1636 m, Ruwenzori, Uganda. The 2 specimens cited here were determined by Fries (Svensk Bot. Tidskr. 22: 366. 1928) as *C. Rueppellii* var. *centrali-africana* R. E. Fr. But this variety is not recognized here even as a minor variant, because the type or "specimen originale" of Fries is another species (cf. *C. Friesii*). It should be noted also that the only other specimen cited under this variety by Fries (*loc. cit.*) is still another species (cf. *C. Mildbraedii*). However, the two specimens of Scott Elliot cited above are transitional toward the next, especially in the short narrow outer involueral bracts.

6. With a single erect remotely branched stem 2–3.5 dm high; branches strictly erect; heads small, about 20-flowered; involucre 8 mm long, 3–4 mm wide at base in fruit; outer bracts $\frac{1}{4}$ – $\frac{1}{2}$ as long as inner bracts, 0.3–0.5 mm wide; corolla 9–10 mm long; ligule 1.25 mm wide, the teeth typical; corolla tube 2.5 mm long, papillose-scabrous from base to summit, as in m.v. 5; anther tube 3.25 mm long, the appendages 0.6 mm long, oblong, acute; style branches 1.75 mm long, 0.1 mm wide, yellow; achenes dark brown in sic., 4.5 mm long, 0.5 mm wide, 13–15-ribbed, shortly and coarsely beaked; pappus white, 4 mm long, 2-seriate, setae equal, fine, falling away easily and singly, as in typical plants. *Dummer 3717* (K) 1515 m, Mt. Elgon, Uganda.

7. Root, leaves, and stems typical, and the inflorescence typical in all details except in the smaller heads and florets and the shorter coarsely beaked achenes. Mature involucre 6 mm long; florets about 9 mm long; achenes 4–5 mm long, marginal ones dorsoventrally compressed, the ribs stronger than in typical forms; pappus 4 mm long. *Greenway and Hummel 7273* (UC, Amani) burnt grassland in open stands of *Acacia* and *Croton* on gray sandy loam; also in open bush, *Combretum*, *Protea*, on a gentle slope, Mt. Lomwaga, 2532 m, S.E. Imatonga, E. Prov., Uganda.

8. Biennial (?), root short, conical; leaves typical; stems robust, nearly erect, 2–3.5 dm high; inflorescences, heads, florets, and pappus typical; achenes 5–6 mm long, shortly and coarsely beaked, the marginal ones dorsoventrally compressed, the ribs stronger than in typical forms. Described by the collector as "a biennial herb with a short carrotlike taproot." Even if it is actually biennial, the difference in length of life cycle does not exclude it from this species. Several species in sec. 25 are known to include annual, biennial and perennial variants. However, the larger flower heads (involucre at least 10 mm long and 4 mm wide at middle), combined with the erect robust stems and the achenes as in m.v. 5 may represent a natural population worthy of recognition as a subspecies, especially if the biennial habit is characteristic. *Greenway and Eggeling 7210* (UC, Amani) common, but scattered among trees in grassland with *Lactuca capensis*, Arua, 1535 m, W. Nile dist., N. Prov., Uganda.

The Uganda Assemblage.—Only 6 collections from the Uganda reg. have been seen by the present author (cf. m.v. 4–8 and *Napier 2184*) and they are from widely separated localities. Minor variants 4–6 seem to exhibit a tendency toward a more erect habit and smaller heads with smaller outer involueral bracts. To what extent these peculiarities are genetic is not known, and at present we do not know whether fully typical plants occur in Uganda. The occurrence of *Napier's* typical plant in W. Kenya, however, would indicate that similar plants may also be expected in Uganda. The possibility should be recognized, however, that a distinct subspecific entity of some sort may exist in Uganda, or may be in process of differentiation; but more material is needed, together with field observations, in order to determine the true situation. These plants, especially the Mt. Elgon spec. (cf. m.v. 6), approach *C. Mildbraedii* of sec. 8 in habit, size of heads and florets, and the narrow outer bracts of the involucre. But the latter species is well separated geographically and differs in important characteristics.

Relationship

Crepis Rueppellii is closest to *C. Forskalii* and *C. abyssinica*, from both of which it is easily distinguished by the longer corolla, anther tube, and style branches, and the larger achenes. Also the leaves in *C. Rueppellii* (except in m.v. 1 and 2, which may be distinct entities) are merely denticulate or dentate, not pinnately lobed as in *C. abyssinica*, and the achenes are definitely beaked. *C. Rueppellii* is less close to *C. xylorrhiza* and *C. tenerrima* and farther still from *C. Friesii* and *C. Mildbraedii* of sec. 8. Although it is a strong-rooted perennial, *C. Rueppellii* is a more advanced species than any of the others mentioned above except *C. Forskalii*.

191. *Crepis Forskalii* sp. nov.

(Fig. 299.)

Herba perennis 1.8–3.5 dm alta; radix recta elongata lignea; caudex brevis 8–10 mm latus; folia caudicalia numerosa interdum 15 cm longa 3 cm lata oblanceolata vel elliptica acuta irregulariter denticulata petiolata tomentulosa vel glabra; folia caulina pauca lanceolata acuminata vel bracteiformia; caules 2–4 flexuosi vel semidecumbentes tenui glabri remote ramosi, ramis elongatis cymosis; pedunculi 0.5–4 cm longi tenuissimi; capitula pauca erecta parva circa 40-flora; involucri cylindrica circa 8 mm alta 4 mm lata, squamis exterioribus circa 8 parvis linearibus fuscis vel purpureis scariosis laxis, interioribus 8–10 lanceolatis obtusis setulosis in maturitate ad basim spongioso-incrassatis ventrale glabris; receptaculum alveolatum breve ciliatum; corolla circa 10 mm longa, ligula circa 7 mm longa 1.25 mm lata, tubo papilloso pilis minutissimis; antherae 3.25 mm longae, filamentis brevissimis delicatis; rami styli circa 1.5 mm longi flavi; achaenia fulva 5–6 mm longa fusiformia in rostrum tenuissimum abrupte constricta 10-striata; pappus albus 3–4 mm longus 1-seriatus tenuis mollis deciduus.

Perennial, 1.8–3.5 dm high; root woody, vertical, elongated, 4–7 mm wide, bearing slender fibers; caudex short, 8–10 mm wide, leafy; caudical leaves numerous, up to 15 cm long or longer, 3 cm wide, oblanceolate or elliptic, acute, irregularly denticulate, denticles corneous-mucronate, attenuate into a rather short winged petiole with broader clasping base, finely tomentulose, glabrescent or glabrous; cauline leaves few, lanceolate-acuminate, linear or bractlike; stem 2–4, flexuous or semidecumbent, slender, terete, striate, glabrous, remotely branched from middle or near base, branches elongated, few-headed, forming an open compound cyme; peduncles 0.5–4 cm long, very slender, tomentulose or glabrescent; heads erect, small, about 40-flowered; involucre cylindric, 8 mm high, 4 mm wide in fruit, \pm tomentose; outer bracts 7–8, longest $\frac{1}{4}$ as long as inner bracts, linear, brown or purplish, becoming scarious, spreading; inner bracts 8–10, lanceolate, obtuse, ciliate at apex, pale green with dark dorsal stripe, margin white, membranous, dorsally setulose with short stout blunt black setules, ventrally glabrous, becoming spongy-thickened near base at maturity, ultimately reflexed; receptacle alveolate, ciliate, cilia very short; corolla about 10 mm long; ligule 1.25 mm wide, teeth 0.2–0.5 mm long, prominently gland-crested and hooded as in *C. Rueppellii*; corolla tube 2–3 mm long, beset with very short (up to 0.05 mm long) papilliform hairs; anther tube 3.25×1 mm dis.; appendages 0.4–0.5 mm long, oblong, \pm obtuse; filaments delicate, very short, scarcely longer than the appendages; style branches 1.5 mm long, 0.1 mm wide, yellow; achenes tawny, 5–6 mm long, fusiform, subcompressed, abruptly constricted into a filiform beak equal to body, constricted above the narrow brown pale-calloused base, 10-striate, striae pale, narrow, finely spiculate; pappus white, 3–4 mm long, 1-seriate, fine, soft, exceeding the involucre, deciduous. Flowering Feb.; flowers yellow, reddish on outer face of ligules.

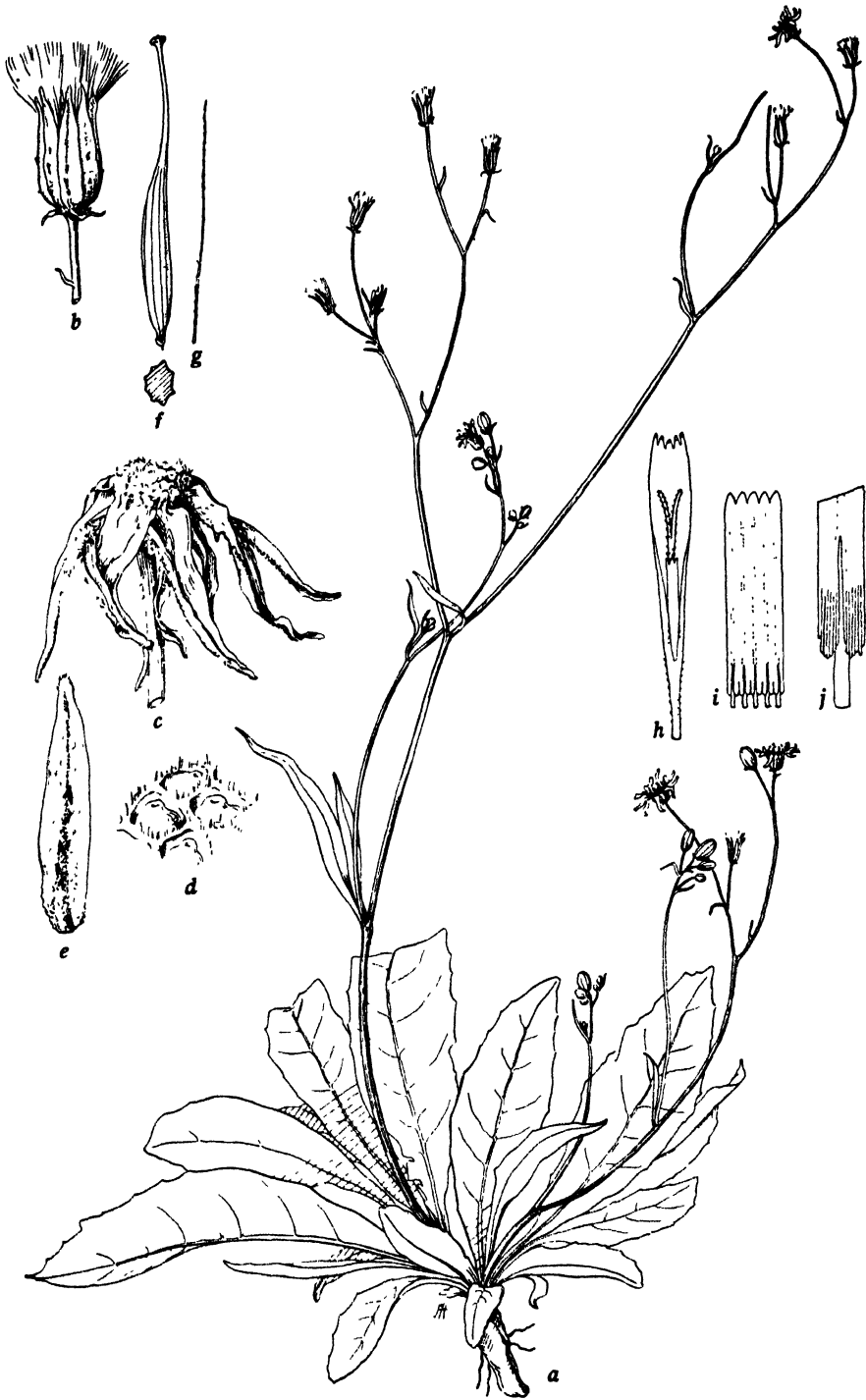


Fig. 299. *Crepis Forskalii*, from type (RB): a, plant, $\times \frac{1}{2}$; b, mature head, $\times 2$; c, old head with reflexed bracts, $\times 4$; d, detail of receptacle, $\times 16$; e, inner involucre bract, outer face, $\times 4$; f, achene and outline of cross section, $\times 8$; g, pappus seta, $\times 8$; h, floret lacking ovary, $\times 4$; i, anther tube, $\times 8$; j, detail of appendages, $\times 32$.

Arabia, Yemen Prov., opposite Eritrea. The type collection, *Schweinfurth 1140*, was taken, according to the labels, at Uosril, elevation 1400 m, on February 9, 1889. It seems highly probable that "Uosril" is either an older form or a misspelling of Usil, a town on the lower border of the coffee belt, the altitude of which is 4300 ft. (= 1300 m) according to *Encyclopaedia Britannica*. This assumption is greatly strengthened by the fact that another collection of this species, *Schweinfurth 1417*, was taken on February 22, 1889 "below and above Menacha, 2000–2500 m." Menacha is undoubtedly a variant of Menakha or Manakha, an important center in the coffee belt which extends from 1200 to 2100 m altitude. These collections are part of a series entitled *In Memoriam Divi Forskalii ex Arabia Felici attulit*.

Monomorphic.

Arabia: Yemen Prov., Uosril (= Usil †), 1400 m, *Schweinfurth 1140* (RB type, K, G, UWG, UCF); Yemen Prov., below and above Menacha (= Menakha, Manakha), 2000–2500 m, *Schweinfurth 1417* (RB, K, UWG); locality † *Forskal 479* (B, UCF).

It should be noted that the Berlin specimen, cited last in the foregoing list, is certainly this species. The label reads "*Crepis radicata* Forsk. Fl. arab. No. 479." As there is no information concerning locality, one of the plants in Schweinfurth's first collection is chosen as the type. It is in the Reuter-Boissier herbarium; the specimens of the same number in the Kew and Gray Herbaria and in the general herbarium of the University of Vienna are isotypes. A photograph of the type is in Herb. Univ. Calif.

Relationship

Crepis Forskalii is closest to *C. Rueppellii*, from which it is very distinct in the more numerous, smaller heads; the shorter, linear outer involucre bracts and the stout, blunt, glandless setules on the inner involucre bracts; the much smaller florets with smaller anther tubes and appendages and shorter style branches; and the shorter achenes with relatively longer beaks and shorter pappus. The two species are very close, however, their differentiation having been due in part, no doubt, to geographic isolation. Both *C. Forskalii* and *C. Rueppellii* exhibit sufficient resemblance to *C. bellidifolia* and the other species of this section to suggest a common ancestry.

192. *Crepis bellidifolia* Loisel.

Fl. Gallica, 527. t. 18. 1806. (Fig. 300.)

Perennial, flowering the first year, 0.35–5 dm high; root straight, elongated, woody; caudex simple, few-leaved and 1-stemmed, or \pm divided, leafy and few- or many-stemmed; caudical leaves up to 11 cm long, 3 cm wide, oblanceolate; entire, dentate, runcinate, or pinnately lobed or parted with close or remote entire or dentate segments, glabrous or pubescent beneath on midvein, the petiole usually short, narrowly winged, broader at base; cauline leaves similar or sessile, auriculate-amplexicaul, uppermost bractlike; stems decumbent or semidecumbent, slender, terete, striate, glabrous or hispidulous near base, simple, 1-headed, or racemously branched beginning near base, the branches remote, elongated, 1–4-headed; peduncles 2–15 cm long, slender, not much thickened at maturity, glabrous or tomentulose near base of head; heads erect, small, many-flowered; involucre 7–10 mm high, 4–5 mm wide at base in fruit, cylindric-campanulate, becoming broader and spongy-thickened at base, ultimately reflexed; outer bracts about 10, nearly equal, longest $\frac{1}{4}$ or $\frac{1}{3}$ as long as inner bracts, linear, glabrous, tomentulose or shortly gland-pubescent; inner bracts 9–13, lanceolate, obtuse, glabrous, tomentulose or shortly gland-pubescent, shortly pubescent on inner face, becoming carinate, infolding the marginal achenes sometimes closely; receptacle areolate, shortly white-ciliate;

corolla 9–10 mm long; ligule 1.7 mm wide; ligule teeth 0.3 mm long, acute, the two lateral pairs of teeth tending to remain united; corolla tube 2 mm long, slender, pubescent with white acicular hairs up to 0.5 mm long; anther tube 2.8×0.9 mm dis.; appendages 0.5 mm long, narrow, acute; filaments 0.4 mm longer; style branches 1 mm long, slender, yellow; achenes 3.5–6.5 mm long, grayish-yellow, yellow or pale brown, slender, fusiform, abruptly or gradually attenuate into a (usually fine) beak $\frac{1}{4}$ – $\frac{1}{2}$ as long as the whole achene, with slightly dilated pappus disk and narrow calloused base, 10-ribbed, ribs fine, finely spiculate; pappus 3–3.5 mm long, white, 1-seriate, very fine, soft, caducous. Flowering May–Aug.; flowers yellow with red on outer face of ligule. Chromosomes, $2n = 8$.

Barkhausia bellidifolia DC., Fl. Fr. 5: 449. 1815.

B. sardoa Spreng., Syst. 4(2): 304. 1827.

B. caespitosa Moris, Fl. Sard. 2: 524. t. 92. 1840–1843.

Crepis caespitosa Gren. et Godr., Fl. Fr. 2: 332. 1850.

C. decumbens Gren. et Godr., loc. cit.

Hieraciodes bellidifolium O. Kuntze, Gen. 1: 345. 1891.

Italy, on the mainland around Livorno (Leghorn); islands of the Tuscan Archipelago; Corsica and Sardinia; and at a few isolated stations in S. France and Spain, including the Balearic Is., according to Barcelo y Combis (Fl. Bal., 291). It is at present doubtful whether this species is indigenous in these more western regions. Unfortunately, its discovery at Mont Louis, France, by the author was not realized until too late to study its distribution in that region. He is under the impression, however, that it was locally abundant.

The type was not seen by me; but the original description and illustration are sufficient to identify a plant from Corsica. If the type of Loiselier does not exist, the specimen of *Robert* in 1808 in herb. DC. Prod. VII: 156 n. 24-3a may be accepted as the type.

The above treatment of synonymy is based on the author's extensive examination of herbarium specimens, supplemented by his collections and field observations in Corsica. Furthermore, it is in complete agreement with the conclusions reached by Sommier (cf. Bull. Soc. Bot. Ital. 1900: 238-244) after similar studies and field observations on the islands of the Tuscan Archipelago. If any of these synonyms deserves to be recognized as a named or numbered form, it is *Barkhausia caespitosa* Moris as represented by his illustration in Fl. Sard. (loc. cit.). But this appears to be only a denticulate-leaved form of the species, although an authentic specimen of Moris' plant has not been seen by either Sommier or the author. Furthermore, as Sommier points out, the Corsican plant distributed as *C. caespitosa* Mor. by Mabilie (no. 247) is typical *C. bellidifolia*.

The notable polymorphism of *C. bellidifolia* is to be accounted for on the basis of both ecological and genetic factors. The ecological factors responsible for wide differences in size and habit of the plants include the whole gamut of environmental conditions and their various combinations. On the other hand, that genetic factors are involved in many of the variations is nicely illustrated by the following observations. At a single station in Corsica the author collected a series of specimens (see Babcock 367, a, b, c, d, and 369 in Herb. UC) which show 5 well-marked differences in their achenes with reference to length, relative length of beak, width of body, and color. No doubt more extensive collections at the same station would bring to light still other differences or combinations of those already noted in the fruits. Furthermore, in garden cultures of 9 strains of this species, grown from seeds collected by the author in Corsica, marked differences in size and dissection of the leaves were noted. Some of the cultures were uniform, whereas others were segre-

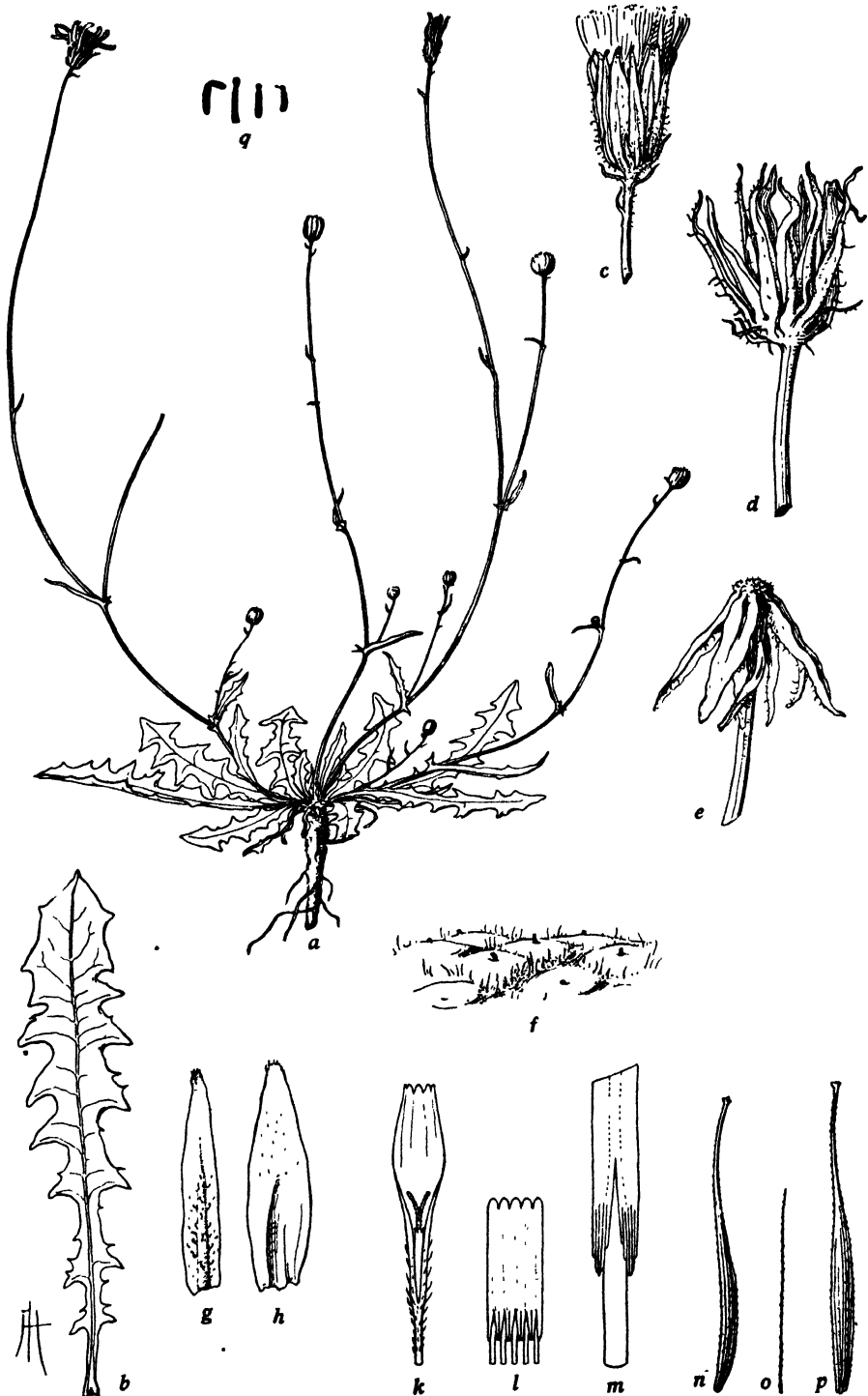


Fig. 300. *Crepis bellidifolia*, a-p, from Babcock 367 (UC 429402); q, from Babcock 361 (UC 429396): a, plant, $\times \frac{1}{2}$; b, caudical leaf, lower face, $\times 1$; c, nearly mature head, $\times 2$; d, old head, $\times 2$; e, head with reflexed bracts, $\times 2$; f, detail of receptacle, $\times 25$; g, h, 2 inner involucre bracts, outer and inner faces, $\times 4$; k, floret lacking ovary, $\times 4$; l, anther tube, $\times 8$; m, detail of appendages, $\times 32$; n-p, 2 achenes and a pappus seta, $\times 8$; q, somatic chromosomes, $n = 4$, $\times 1250$.

gating. In view of the genetic and environmental diversity affecting the phenotypic variability of this species, the futility of attempting an extensive listing even of serially numbered variants must be obvious. The necessity, however, of mentioning two such variants below is made clear in connection therewith.

Italy: Tuscany, Livorno, grassy places near the sea from Marzocco to the Calambrone (acc. to Sommier, *loc. cit.*, whose specimens in Herb. Fl. were seen by the author. **Tuscan Archipelago:** "insulis Etruriae," Savi in 1839 (K); Gorgona, maritime rocks, Savi in 1836 (K); Capraja, around the city, Bicknell in 1903 (Bur); Elba, Golfo Stella, Sido, Sommier in 1900 (Bur). **Corsica:** no definite locality, Robert in 1808 (DC); near Ajaccio, Burnat *et al.* 181 (Bur); Serra di Scopameme near Sartene, Reverchon 161 (K, Ms); Cap Corse, tree-covered slopes near Mandriale, Mabilie in 1867 (G, US); Mt. Pigno, at the glacier, Mabilie 247 (K, Bo, Bur, G); Mt. Cinto, above Calacuccia, upper limits of agriculture, Levier in 1880 (Bo); Bonifacio, near seashore, Stephani in 1914 (Bur); Mt. Pigno, summit, Debeaux in 1869 (Ms); above Vizzavona, Babcock 367, 369 (UC); between Calvi and Ajaccio, Babcock 361 (UC); Grossetta, between Ajaccio and Sartene, Babcock 363 (UC); Corte, trail to Gorge du Tavigliano, Babcock 371, 372 (UC); near Zonza, Babcock 366 (UC); above Bastia, Babcock 373 (UC); Iles Sanguinaires, Salzmann in 1821 (DC, Ms, K, G) m.v. 1; *ibid.*, J. Gay in 1848 (K, UCf) m.v. 1. **Sardinia:** no definite locality, Boderio in 1824 (DC); Santa Teresa Gallura, near Tempio, Reverchon 56 (K, Fl, G, Bur, BML, US); Gulf of Palma, Forsyth-Major 43 (Fl); Mt. Oliena, lower altitudes, F. Major in 1884 (Bo, Bur); Maddalena I., Vaccari in 1907 (Fl). **France:** Nice, Carabacel, Sarato in 1867 (Fl, UCf); Toulon, Cap Brun, Metz ? in 1870 (Bur, UCf) m.v. 2; Herault, route to Ganges, 6 km from Montpellier, Fehlmann in 1895 (Ms); Pyrenees, near Mont Louis, Babcock 398 (UC). **Spain:** Alicante, around Denia, Porta *et Rigo* 392 (K, Bur); Balearic Is., Majorca, near Palma, Sierra Burguesa (very rare acc. to Barcelo y Combis, Fl. Bal., 291), not seen by the author.

Minor Variants of *C. bellidifolia*

1. Achenes only 3–4 mm long; marginal achenes obcompressed and whitish on inner face, not beaked, slightly longer than inner achenes; inner achenes finely beaked, beak equal to body. The collections of Salzmann and J. Gay are closely similar, except that Gay's specimen is somewhat taller. The following additional description will show that this is a distinct form of *C. bellidifolia*. Certainly it differs in other primordia as well as in the achenes; but whether it is a sufficiently distinct form to warrant its recognition as a subspecies is at present doubtful. Information is needed concerning variability in the indigenous population. In view of the paucity of herbarium material of this variant and the lack of field observations, the present treatment seems justified. Plant annual (?), glabrous except involucre tomentulose; root slender; caudical leaves oblanceolate, runcinate, somewhat fleshy; stems several, decumbent, terete, reddish near base, racemously branched; peduncles somewhat thickened near head; involucre 9 mm high, 5 mm wide near base in fruit, becoming spongy-thickened; inner bracts pubescent within; receptacle areolate, white-ciliate; corolla 9–10 mm long; style branches 1 mm long, fine, yellow; pappus 3 mm long, very fine, caducous. Salzmann in 1821 (DC, Ms, K, G), Iles Sanguinaires, Corsica; J. Gay in 1848 (K), Iles Sanguinaires, Corsica.

2. Marginal achenes not beaked, at least some of them laterally compressed and gradually attenuate upward. Caudical leaves up to 9 cm long, 1 cm wide, oblanceolate, acute, denticulate to runcinately dentate, petiole narrowly winged; cauline leaves up to 3 cm long, 0.5 cm wide, lanceolate, acuminate, sessile, amplexicaul, acutely auriculate; stems numerous, very slender, decumbent, up to 20 cm high, 1–2 furcate, 2–4 headed; petioles 4–15 cm long; involucre 8 mm high, 4 mm wide near base, canescent-tomentose; bracts and receptacle typical; florets 8 mm long; style branches yellow; achenes 4.75–5.5 mm long, pale brown, marginal ones gradually attenuate, not beaked, laterally compressed, ventrally angled, unequally ribbed, constricted at the narrow base with small oblique scar, inner ones subterete, gradually attenuate into a slender beak nearly equal to body, 10-ribbed, ribs finely spiculate; pappus 3.5 mm long, 1-seriate, fine, caducous. Flowering June; flowers yellow. Metz ? in 1870 (Bur), roadside, Cap Brun, near Toulon, France.

Relationship

C. bellidifolia has no very close relatives. In its karyotype it shows most resemblance to *C. amplexifolia* and *C. bursifolia*, from both of which it is very distinct in gross morphology. Reduced plants of *C. vesicaria*, especially the low slender decumbent forms sometimes found on seashores, are easily mistaken for *C. bellidifolia*, but the latter is clearly distinguished by the linear outer bracts of the involucre,

the shorter pappus, the yellow style branches, and the glabrous leaves. That *C. bellidifolia* is a more advanced species than *C. vesicaria* is indicated by the marked reduction in bracts, florets, and achenes, as well as in size of the plant itself.

193. *Crepis bursifolia* L.

Sp. Pl. 2: 805. 1753. (Fig. 301.)

Perennial, 0.5–3.5 (mostly 1–2) dm high; root vertical, elongated, woody, up to 0.5 cm wide; caudex up to 1 cm long, 1 cm wide, pitted with old leaf scars or brown bases of old leaves, simple or shortly furcate; caudical leaves numerous, 2.5–25 cm long, 0.6–5 cm wide, oblanceolate, obtuse or acute, lyrate-pinnatifid, terminal segment usually larger, ovate-truncate, lateral lobes lanceolate, acute, all segments denticulate or dentate, teeth corneous-mucronate, leaves sometimes pinnately parted, the lateral segments remote, occasionally with the terminal lobe as small as the lateral (m.v. 1), leaves rarely entire, always glabrous or puberulent; cauline leaves mostly small, linear or bractlike; stems 2–9 or more, decumbent or arcuate, slender, terete, striate, glabrous, tomentulose or sparsely pubescent, cymosely 2–5-branched near summit, the branches strict, pedunculate or 2–4-headed with short peduncles; peduncles and involucre canescent-tomentose; heads erect, small, 30–60-flowered; involucre cylindric, 8–11 mm long, 3–4 mm wide at middle, setulose with pale yellow mostly glandless hairs on outer and inner bracts, or sometimes shortly and finely gland-pubescent, sometimes merely tomentose; outer bracts 10–14, about $\frac{1}{3}$ as long as the inner, linear, acuminate, lax; inner bracts 10–12, lanceolate, acute, white-ciliate at apex, paler in mid-region, darker toward margin, appressed-pubescent and with a prominent pale median nerve on inner face, becoming strongly carinate, pale spongy-thickened and swollen at the base, ultimately reflexed; corolla 10–11 mm long; ligule 1.4 mm wide, pubescent toward base; teeth 0.2 mm long; corolla tube 2.25 mm long, pubescent with 2–3-celled acicular hairs; anther tube about 3.5×1 mm dis.; appendages 0.4–0.5 mm long, lanceolate, acute, united; style branches about 1.3 mm long, 0.1 mm wide, green; achenes pale brown, 5.5–7 mm long, the body about 2.5 mm long, 0.4 mm wide, fusiform, abruptly attenuate into a pale filamentous fragile beak nearly twice as long as the body, with expanded pappus disk 0.2–0.3 mm wide, narrowed toward the finely calloused hollow base, 10-ribbed, ribs narrow, rounded, finely spiculate; pappus white, 3–4 mm long, 2–3-seriate, extremely fine, soft, deciduous. Flowering time about 2 months during the period April–Sept., acc. to climate; flowers light yellow, the ligules livid (i.e., greenish- or bluish-gray) on outer face, turning dark green or purple when withered. Chromosomes, $2n = 8$.

Hyoseris hirta Balb., ex Willd., Sp. Pl. 3: 1614. 1800.

Crepis hirta Pers., Syn. Pl. 2: 377. 1807 non L.

Lagoseris bursifolia Lk., ex Reichenb., Icon. Bot. Comment. cent. 1: 29. f. 64. 1823.

Barkhausia bursifolia Spreng., Syst. 3: 653. 1826.

B. canescens Spreng. loc. cit.

Leontodon Gussonei Spreng., op. cit., p. 658.

B. Balbisiana DC., Prod. 7: 155. 1838.

C. Balbisiana F. Schultz, Flora 23: 718. 1840.

C. erucaeifolia Gren. et Godr., Fl. Fr. 2: 331. 1850 non Tausch.

Hieraciodes bursifolium O. Kuntze, Gen. 1: 345. 1891.

Endemic in Italy, acc. to Fiori (432), occurring on the mainland in Toscana and Campania, also in Sicily. Acc. to Gussone (Fl. Sic. 2: 408. 1843), it occurs in Sicily on both calcareous and volcanic formations, on dry hills, and along roads. One of Gussone's localities, Nicosia, has an elevation of about 900 m. Introduced into S. France about 1850 (acc. to Thellung, Mitt. Bot. Mus. Univ. Zurich 18: 585. 1912),

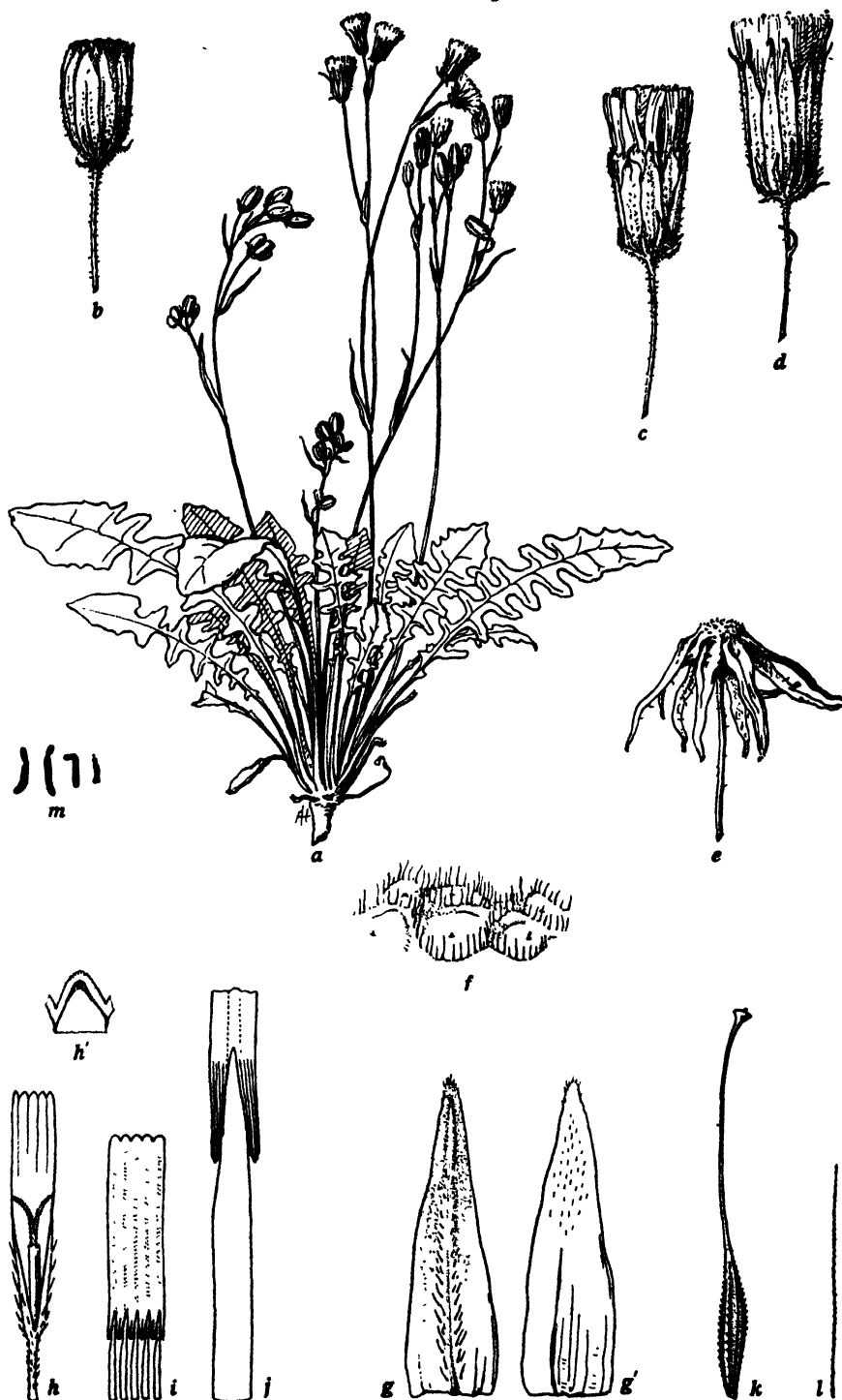


Fig. 301. *Crepis bursifolia*, from Hall 12528 (UC 346494); m, from hort. genet. Calif. 1220 (grown from seeds received from Palermo Bot. Gard.): a, plant, $\times \frac{1}{2}$; b-e, heads, $\times 2$; f, detail of receptacle, $\times 25$; g, g', inner involucre bract, outer and inner faces, $\times 4$; h, floret lacking ovary, $\times 4$; i, detail of ligule tooth, $\times 25$; j, anther tube, $\times 8$; k, l, detail of appendages, $\times 32$; k, l, achene and pappus seta, $\times 8$; m, somatic chromosomes, $n = 4$, $\times 1250$.

it has become naturalized in the coastal region from Var to Hérault. It is reported from Dalmatia by Markgraf (862), where it is probably adventive; and it has been collected by the author near wharves in Tunis. Introduced at Berkeley about 1920, it has already become established on the campus of the University of California. It must be recognized as an aggressive weed in environments to which it is adapted.

This species has been illustrated in numerous publications, including the one first cited by Linnaeus in his original description as *Hieracium siculum, bursae pastoris folio*, Bocc., Mus. 2: 247. t. 106 et 112. I have no record that the type exists in the Linnaean Herbarium; but I have seen the authentic specimen of Bocconio cited by Linnaeus. It is in Herb. Bot. Mus. München (ex herb. Schreber). Except for such size variations as those recorded in the above description, the species is remarkably uniform.

Italy: Campania Prov., Gaëta, Tenore in 1833 (DC); Toscana Prov., E. base of Mt. Argentario, near Orbetello, Levier in 1873 (UC); Sicily, Gussone in 1831 (DC), as *Leontodon Gussonei*; without locality (in hort. Taurin. ?), Balbis in 1805 (DC), as *Hyoseris hirta* Willd.; Sicily, Palermo Gussone in 1825 (DC); Palermo, roads and dry fields, lower and montane regions, Ross in 1898 (K); Syracuse, near Avola, Rigo 192 (US). **France:** Var, Toulon, Huet in 1870-1874 (Bur, K, US); Var, St. Pauline, on ballast between railroad tracks, Hall 12528 (UC); Var, Carnoules, between railroad tracks and platform, shaded below, Hall 12531 (UC); Marseille, field borders, Chamboun (DL), as *C. erucaefolia*; Bouches-du-Rhône, Pas des Lanciers, Antheman in 1880 (K, Rome); Hérault, Montpellier and Lunel, Sennen in 1894 (Ms, UC) m.v. 1; Gironde, Bordeaux, Alleizette in 1930 (UC). **Tunisia:** Old port near site of Carthage, Babcock 269 (UC).

Minor Variant of C. bursifolia

1. Leaves finely dissected with cuneate lobes, the terminal lobe no larger than the lateral ones. Sennen in 1894 (Ms, UC) Montpellier and Lunel, Hérault, France.

Relationship

Crepis bursifolia, like *C. bellidifolia*, is a perennial plant and is less reduced in size of heads, flowers, and fruits than the following species of this section. The achenes of *C. bursifolia*, however, are more like those of *C. senecioides*, especially in the long, filamentous beak, although the body of the achene in *C. bursifolia* is terete or only slightly compressed. Also, the stricter habit of the plant, especially the branchlets and peduncles, suggests closer relationship with *C. senecioides* than with the other species in this section.

194. *Crepis nigricans* Viv.

Fl. Lib. 51. t. x. f. 3. 1824. (Fig. 302.)

Annual, 0.5-1.5 dm high; root vertical, slender; caudex slightly swollen, leafy; caudical leaves up to 10 cm long, 1.5 cm wide, oblanceolate, acute, corneous-mucronate, denticulate to runcinate-pinnatifid, gradually attenuate into a short winged petiole with broader clasping base, puberulent with fine short white glandless hairs or glabrescent, margin shortly ciliate; cauline leaves similar or acuminate, sessile, base rounded-amplexicaul, sometimes lacinate, uppermost bractlike; stems several, slender, fistulose, spreading or semidecumbent, or only one, erect, remotely branched from near base, branches elongated, usually cymosely branched near summit, 1-3-headed, like stem finely hispidulous with pale glandless hairs; peduncles 0.5-4.5 cm long, very slender, erect, little changed in fruit, canescent-tomentulose, sparsely hispidulous, shortly pubescent with greenish gland hairs; heads erect, small, many-flowered; involucre cylindric-campanulate, 6-7(8) mm high, 2-3 mm wide near base in fruit, canescent-tomentulose, shortly gland-pubescent, sparsely setulose with long black mostly glandless setules; outer bracts 6-10, linear, pale, about $\frac{1}{2}$ as long as inner ones; inner bracts 12-14, lanceolate, obtuse, white-ciliate at tip,

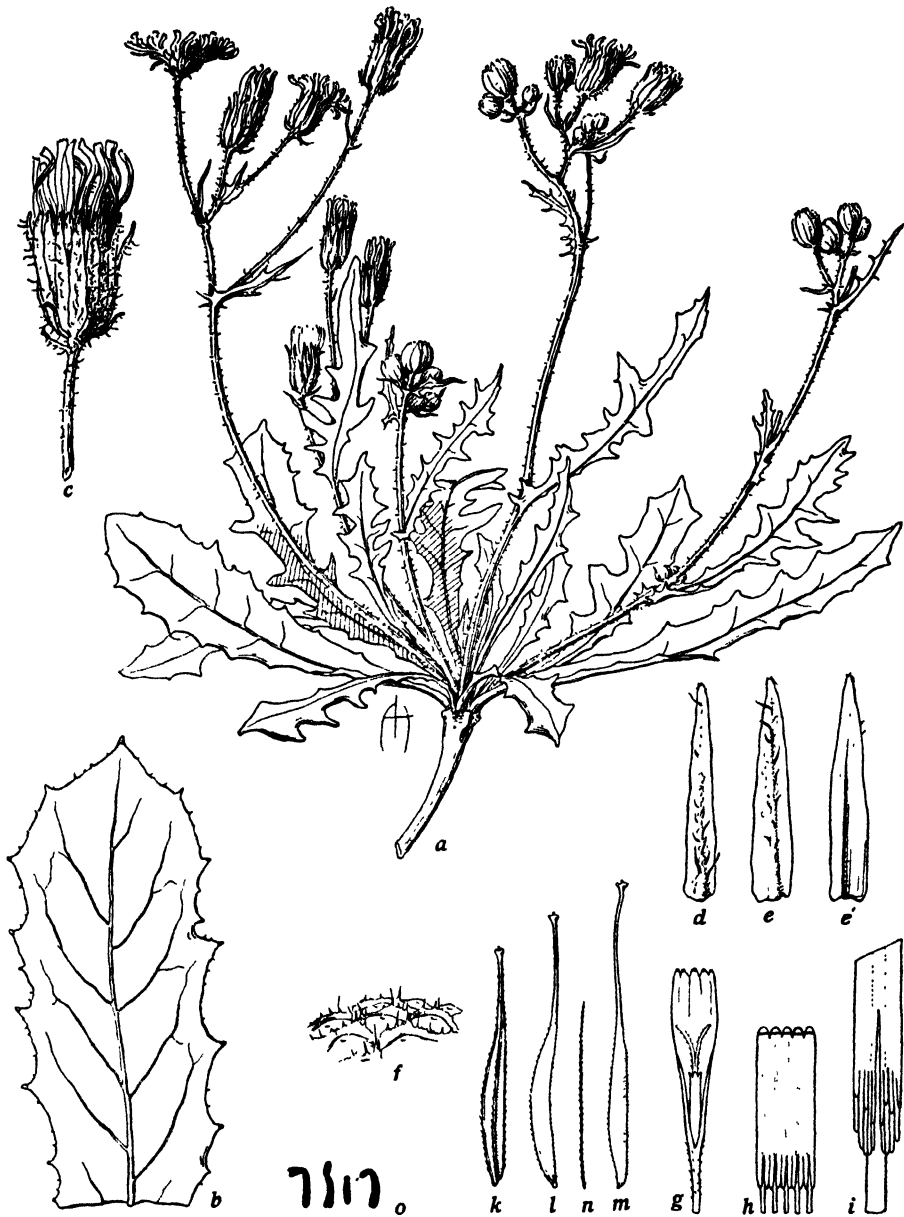


Fig. 302. *Crepis nigricans*, a–h, l–n, from Fenzi in 1931 (UC 463900); k, from Pitard 175 (K); o, from hort. genet. Calif. 3020 (grown from seeds collected near Tripoli by Signora E. Fenzi; cf. UC 463900): a, plant, $\times 1$; b, upper half of a caudical leaf, lower face, $\times 2$; c, flower head, $\times 2$; d, e, e', 2 inner involucre bracts, $\times 4$; f, detail of receptacle, $\times 25$; g, floret lacking ovary, $\times 4$; h, anther tube, $\times 8$; i, detail of receptacle, $\times 32$; k–n, 3 achenes and a pappus seta, $\times 8$; o, somatic chromosomes, $n = 4$, $\times 1250$.

pubescent on inner face, becoming dorsally carinate, spongy-thickened, ultimately reflexed; receptacle alveolate, alveolae 0.3–0.4 mm wide, fimbriae low, membranous, finely ciliate, cilia 0.2–0.3 mm long; corolla in marginal florets 8 mm long; ligule 1.5 mm wide, ligule teeth 0.15–0.25 mm long; corolla tube 2 mm long, rather stout, sparsely beset with short (up to 0.2 mm) acicular hairs; anther tube 2.6×1 mm dis.; appendages 0.6 mm long, oblong, rather obtuse, partly united; filaments short, stout; style branches 1–1.5 mm long, 0.1 mm wide, yellow; achenes biform, tawny or pale yellow, 3.5–5 mm long; marginal achenes a little shorter than inner ones, laterally compressed, more coarsely beaked; inner achenes fusiform, constricted at the narrow obliquely calloused base, attenuate into a fine pale beak $\frac{1}{3}$ – $\frac{1}{2}$ the length of whole achene, with expanded pappus disk, 10-ribbed, ribs narrow, rounded, spiculate; pappus white, 3 mm long, 1-seriate, very fine, soft, deciduous. Flowering March–April; flowers yellow, reddish-purple on outer face of ligule in marginal florets. Chromosomes, $2n = 8$.

Crepis nudiflora Viv., Fl. Lib. 51. t. xiii. f. 2. 1824, cf. m.v. 1.

Barkhausia radicata var. *Kralikii* Pomel, Nouv. Mat. Fl. Atl. 5. 1874.

C. Kralikii Pomel, op. cit., 261 in nota. 1875, cf. m.v. 2.

C. senecioides Del., ex Batt. et Trab., Fl. Alg. 561. 1888–1890.

C. radicata fa. *nigricans* (Viv.) Pamp., Bull. Soc. Bot. Ital. 5: 5. 1921.

Mediterranean littoral, locally from S. Tunisia to Egypt; sandy wastes and oases.

Rather variable in size of plant and in the achenes, especially in respect to relative length of beak and body and in comparative width of beak. With reference to these features, 3 outstanding variants are mentioned below.

Libya: Cirenaica, in mountains, *Viviani* (Genoa) type; Cirenaica, meadow, *Viviani* (Genoa) m.v. 1: Tripolitania, Tripoli, among palms to east of city, *Letournem* in 1886 (PC, UCf); Tripoli, near oasis about 3 km from new wall of city, *Miss Fenzi* in 1931 (UC); *ibid.* (UC), m.v. 3; *ibid.*, near city in sand, *Miss Fenzi* in 1933 (UC). **Tunisia:** Gabes, sandy olive orchard, *Kralik 397* (PC, K, Fl) m.v. 2; Gabes, *Kralik* (G, Alger, UC); Zarzis, *Letournem* in 1886 (PC, Fl); Gabes, Kanzeria, desert sands, *Pitard 175* (K, B). **Egypt:** Cairo, lupine field in Ala Roash, *Ascherson 185* (B).

Minor Variants of *C. nigricans*

1. (*C. nudiflora* Viv., loc. cit.) Fruiting heads 8 mm high; achenes 3.5–4 mm long, but with relatively longer and finer beaks than in the type, the marginal ones similar to inner ones; pappus 2–2.5 mm long. (This is not *C. senecioides* Del.) *Viviani* (Genoa) meadow, Cirenaica.

2. (*C. kralikii* Pomel, loc. cit.) Heads rather small; inner involucre bracts 8–13, about 5 mm long; achenes 3–4 mm long, but more abruptly attenuate into the beak and more prominently spiculate throughout; pappus 3 mm long. *Kralik 397* (PC, K, Fl) sandy olive orchard, Gabes, Tunisia.

3. Achenes definitely coarser than in the type, although generally similar. *Miss Fenzi* in 1931 (UC), growing with typical form near oasis about 3 km from new wall of Tripoli, Tripolitania.

Relationship

Crepis nigricans is nearest to *C. filiformis*, from which it is very distinct in the several-headed stems, narrower heads, much longer obtuse anther appendages, shorter and essentially biform achenes, and shorter pappus. It is close also to *C. senecioides*, from which it is even more distinct in the achenes, as well as in other characters.

195. *Crepis filiformis* Viv.

Fl. Lib. 51. t. xxi. f. 1. 1824. (Fig. 303.)

Annual ?, low, spreading; root vertical, slender; caudex slightly swollen, leafy; caudical leaves oblanceolate, acute, corneous-mucronate, sinuate-dentate to runcinate-pinnatifid, attenuate into a short winged petiole, puberulent with short white glandless hairs or glabrate, margin shortly ciliate; cauline leaves none or mostly

reduced, bractlike; stems mostly pedunculate, very slender, spreading; heads erect, small, many-flowered; involucre campanulate, about 8 mm long, 6 mm wide in fruiting heads, canescent-tomentose, sparsely gland-pubescent, setulose with black glandless setules; outer bracts 6, linear, $\frac{1}{2}$ as long as inner bracts, pale, scarious; inner bracts 14, lanceolate, obtuse, ciliate at tip, pubescent on inner face, becoming



Fig. 303. *Crepis filiformis*, a-g, from type (Genoa); h-p, from *Barbey 33* (DL): a, plant, \times ca. 1 (from Viviani, Flor. Lib. tab. xxi, fig. 1); b, part of a leaf, \times 2; c, head and peduncle, \times 2; d, inner involucre bract, inner face, \times 4; e, floret lacking ovary, \times 4; f, anther tube, \times 8; g, detail of appendages, \times 32; h, head, \times 2; i, floret lacking ovary, \times 4; j, anther tube, \times 8; k, detail of appendages, \times 32; l, mature head, \times 2; m, detail of receptacle, \times 25; n-p, marginal and inner achenes and a pappus seta, \times 8.

dorsally carinate, spongy-thickened at base; receptacle alveolate, alveolae 0.2–0.3 mm wide, fimbriellae membranous, coarsely ciliate, cilia 0.2–0.3 mm long; corolla in marginal florets 7–8.5 mm long; ligule 1 mm wide; ligule teeth 0.2–0.3 mm long; corolla tube 2.5–3 mm long, densely beset with stout acicular hairs mostly 0.05 mm long (on base of ligule up to 0.1 mm long); anther tube 2.5 \times 1 mm dis.; appendages 0.3 mm long, lanceolate, acute; filaments 0.5–0.7 mm longer; style branches 1 mm long, 0.1 mm wide, yellow; achenes uniform, pale tawny, 5–5.5 mm long, very slender, subterete, constricted at the dark brown calloused somewhat oblique base,

gradually attenuate into a delicate beak nearly equal to body, with expanded pappus disk, 10-ribbed, ribs narrow, rounded, finely spiculate; pappus white, 4 mm long, 1-seriate, very fine, soft, deciduous. Flowering (?); flowers yellow, reddish-purple on outer face of ligules in marginal florets.

Crepis radicata Forsk., ex Pampanini, Bull. Soc. Bot. Ital. 5: 5. 1921 non Forsk.

Mediterranean littoral in Libya. Known to me from only 2 collections; but some of the localities in Libya, listed by Pampanini under "*C. filiformis et nudiflora* Viv." (Prod. Fl. Cyren. 484-485. 1930), may hold good for this species.

Monomorphic.

Libya: Cirenaica, *Viviani* (Genoa, UCf) type; Cirenaica (- Tripolitania), Tripoli, in desert, *Barbey 33* (DL, UCf).

Relationship

Crepis filiformis is closest to *C. nigricans*, from which it is very distinct in the pedunculate filiform stems, broader campanulate heads, much shorter acute anther appendages, uniform longer and more gradually attenuate achenes, and longer pappus. It is less close to *C. senecioides*.

196. *Crepis senecioides* Delile

Fl. Egypte 118. t. 42. f. 2. 1813. (Fig. 304.)

Annual, 0.1-3 dm high; root very slender; caudex \pm swollen, leafy; caudical leaves rosulate, from very minute up to about 10 cm long, oblanceolate, acute, denticulate to runcinate-pinnatifid with triangular or lanceolate acute segments, the lobes or teeth corneous-mucronate, ciliate, gradually attenuate into a winged petiole, sparsely pubescent, sometimes tomentulose; cauline leaves few, similar to the caudical, or sessile, lanceolate and acuminate, or bractlike; stems few or numerous, from extremely fine up to 2 mm thick near base, tomentulose, often finely gland-pubescent near base, sometimes setulose with pale glandless setules, semidecumbent to strict, paniculately 3-5-branched from below or near the middle, branches 1-8-headed, heads arranged in corymbiform cymes; peduncles 0.2-5 cm long, slender to extremely fine, tomentulose, sometimes finely gland-pubescent; heads erect, small, 20-40-flowered; involucre in fruiting heads 5-10 mm long, 2-3 mm wide at middle, pale or dark green, canescent-tomentulose, sparsely beset with short black glandless setae; outer bracts about 8, linear, 0.2-0.4 mm wide at base, about $\frac{1}{4}$ as long as inner bracts, becoming scarious and lax; inner bracts 8, lanceolate, acute, membranous-margined, glabrous on inner face, becoming rounded-carinate dorsally, pale spongy-thickened near the base, ultimately reflexed; receptacle areolate, very shortly ciliate or glabrescent; corolla 5-8 mm long, ligule 1.25 mm wide; teeth 0.2-0.4 mm long; corolla tube 1.2-2.3 mm long, pubescent with minute (up to 0.1 mm long) acicular hairs; anther tube (2) 3.25×0.8 (0.9) mm dis.; appendages 0.25-0.65 mm long, oblong, acute or obtuse; filaments 0.25-0.5 mm longer; style branches 1-1.4 mm long, 0.1 mm wide, yellow; achenes light or dark brown with a long filamentous pale beak, 4.5-7.5 mm long including the beak, the body 1-1.75 mm long, 0.4-0.7 mm in greatest width, mostly strongly compressed, 10-ribbed, ribs narrow, pale, strongly spiculate, the body constricted at the small pale-calloused base, strongly attenuate at apex, the beak \pm funnel-shaped at the summit, the pappus disk about 0.2 mm wide; pappus white, 1.5-3 mm long, 2-3-seriate, extremely fine, caducous. Flowering March-April; flowers pale yellow, the outermost ligules with or without reddish-purple on outer face. Chromosomes, $2n = 8$.



Fig. 304. *Crepis senecioides*, a, b, from type (Ms); c-h, from hort. genet. Calif. 28.1044 (UC 489398); k-q, from Cavara in 1925 (UC 277222); r, from hort. genet. Calif. 2061 (grown from seeds collected in Egypt by M. J. Hefnaui): a, b, leaf and part of inflorescence, $\times 1$; c, plant, $\times 1$; d, floret lacking ovary, $\times 4$; e, anther tube, $\times 8$; f, detail of appendages, $\times 32$; g, g', h, achenes and a pappus seta, $\times 8$; k, plant, $\times 1$; l, head, $\times 2$; m, floret lacking ovary, $\times 4$; n, anther tube, $\times 8$; o, detail of appendages, $\times 32$; p, p', q, achene and a pappus seta, $\times 8$; r, somatic chromosomes, $n = 4$, $\times 1250$.

Barkhausia senecioides Spreng., Syst. 3: 652. 1826 excl. Balb. syn.

Psammoseris senecioides Boiss., Diagn. ser. 2, 11: 52. 1849.

P. arabica Boiss. et Heldr., Diagn. loc. cit.; *Crepis arabica* Boiss., Fl. Orient. 3: 853. 1875.

Hieraciodes senecioides O. Kuntze, Gen. 1: 346. 1891.

C. radicata Forsk., ex Pamp., Nuovo Gior. Bot. Ital. n.s., 24: 158. 1917 non Forsk.

N. African-Mediterranean littoral from S. Tunisia to the Gulf of Suez, and in Egypt south to Luxor and the Arabian Desert; Arabia in the Sinai Pen. and near the S.E. border of Palestine; Palestine northward to Jaffa and Jericho (this limit acc. to Post, 156).

The type, collected near Cairo, Egypt, is cited below. This species was confused by Muschler (Man. Fl. Egypt 2: 1067. 1912) with *C. radicata* Forsk., which is a synonym of *Picris coronopifolia* DC (cf. Pampanini, R., Bull. Soc. Bot. Ital. 1926: 103). It became the type species of Boissier's genus, *Psammoseris*, which was distinguished from *Crepis* only by the achenes. These are more strongly compressed than those of any other species of *Crepis*, and the beak is filamentous and usually whitish. But Boissier (853) noted that the beak is sometimes reddish-brown in this species and that other *Crepis* species have subcompressed fruits. Certainly the achenes of this species are not typical of *Lactuca*; and the plant in all other respects is typical of *Crepis*. The marked compression of the fruits and the filamentous beak are merely extreme expressions of a trend of specialization which is present in less marked degree in related species. It is of interest to note that, in addition to their extreme morphological specialization, the tiny fruits of this very precocious desert annual retain their ability to germinate for at least 12 years.

This interesting species exhibits an extraordinary range of variation in size of the plant and its parts. Under desert conditions it is sometimes reduced to tiny plantlets only 1 or 2 cm in diameter which, however, are able to produce flowers and fruits. With plenty of moisture it is capable of reaching a height of 3 dm, producing numerous comparatively strong stems and very numerous heads. Although most of this variation may be due merely to environmental differences, yet it is possible that morphologically distinct ecotypes exist. At present, however, we have no basis for the recognition of ecotypes or subspecies. The morphological differences noted under m.v. 1 are known to occur also in other regions besides Palestine; and fairly robust plants have been collected in Egypt where the very low extremely slender form is most common.

Tunisia: between Sfax and Gafsa, Makuassy, *Chabrolin* in 1932 (UC) m.v. 3. **Cirenaica:** Bengasi, *Zunon* in 1916-1917 (Fl) m.v. 3 and 4; *ibid.*, *Petrovich* 132 (UWG) m.v. 3; *ibid.*, *Euhmer* 224 (B) m.v. 3; *ibid.*, *Taubert* 192 (RB); *Rolmeito*, *Vaccari* 188 (Fl); Bosco Gorda, *Cavara* in 1925 (UC); Apollonia, ex hort. genet. Calif. 41.3476 cult. from seeds collected by Maire in 1938 (UC). **Egypt:** near Cairo, sandy road, *Delile* (Ms, UCf) type; ex hort. genet. Calif. 28.1044, cult. from seeds collected at Mouderieh in 1920 (UC); Cairo, *Ascherson* in 1879 (Ms), as *C. radicata* Forsk.; near Abn Zabel, *Schimper* in 1835 (DC) m.v. 2; Pyramids, *West* in 1825, 1835 (DC, K, CA); *ibid.*, *Boissier* in 1846 (RB); *ibid.*, *Schimper* 9 (CA) m.v. 2; near Alexandria, *Mariout*, *Letourneux* in 1878-1879 (K, RB, Rome); between Cairo and Keneh, near Kodah, *Schweinfurth* 357 (B); Luxor, in desert, *Muschler* in 1906 (K); N.W. shore, *Mirza Matruk* (Matruh), *J. Ball* in 1904 (K); middle Egyptian desert, Arabian side, edge of desert near El Ejam, *Schweinfurth* 24 (K). **Arabia:** Petra, *Boissier* in 1846 (RB, UCf), as *C. arabica* = m.v. 1.

Minor Variants of *C. senecioides*

1. (*C. arabica* Boiss., loc. cit.) Acc. to Boissier, distinguished from typical *C. senecioides* by the shorter leaves, more ramose stems, the densely setulose involucre and the gland-pubescent peduncles. In none of these characters, however, does it fall outside the limits of the species. *Boissier* in 1846 (RB), Petra, near the S.E. boundary of Palestine, Arabia.

2. (*C. senecioides* var. *minima* Schimp. in herb.) Merely the most extremely small form; the whole plant only 1-1.5 cm in height and spread. *Schimper* 9, in 1835 (DC, CA), near Abn Zabel, Egypt.

3. (*C. senecioides* fa. *gigantea* Pamp., Nuovo Gior. Bot. n.s. 24: 158, 1917.) Merely the most robust form; stems up to 3 dm high; involucre 10 mm long. *Zunon* in 1916–1917 (Fl) Bengasi; *Petrovich 138* (UWG) and *Ruhmer 224* (B), Bengasi, Cirenaica; *Chabrolin* in 1932 (UC), Makuassy, between Sfax and Gabes, Tunisia.

4. (*C. senecioides* var. *nuda* Pamp., loc. cit.) Merely deficient in the black involucre setules which are characteristic of the species. *Zunon* in 1916–1917 (Fl) Bengasi; *Pampanini 795* (Fl), Cafis, near Bengasi, Cirenaica.

Relationship

Crepis senecioides has the most highly specialized achenes of all the known species in this genus. The average length of the body of the achene is about the same as the average length of the achenes of *C. parviflora*; and the strong compression of the fruits in *C. senecioides*, together with the long filamentous beak and the very short extremely fine pappus, characterizes the high degree of specialization mentioned above. Although *C. senecioides* has 4 pairs of chromosomes, they are definitely shorter than those of *C. nigricans* or *C. bursifolia*.

INTERSPECIFIC HYBRIDS OF *CREPIS* WHICH HAVE BEEN GIVEN LATIN NAMES

× *C. artificialis* Collins, ex Collins, Hollingshead and Avery, Genetics 8: 306, 310-315. 1929. *C. biennis* ($n=20$) × *C. setosa* ($n=4$). A strain derived from a single F_4 plant with 24 chromosomes (20 of *C. biennis* + 2 pairs of *C. setosa*) which was selected in 1926. In 1929 it was described as a constant strain the distinguishing features of which are summarized as follows (cf. *op. cit.*, 312): annual; stem 3-6 dm high, semi-stout, less leafy than *C. setosa*, branched above; caudical leaves rough-hairy, petiolate, lyrate (like *C. setosa*); cauline leaves narrow (like *C. biennis*) auriculate-amplexicaul (like *C. setosa*); peduncles stout (like *C. biennis*), hispid (like *C. setosa*); flower heads (in anthesis) as large as *C. biennis*; involueral bracts carinate and pubescent, as in *C. setosa*; corolla without red on outer face of ligule, as in *C. biennis*; style branches blackish-green, as in *C. setosa*; achenes 4-5 mm long, fusiform, as in *C. setosa*, but beakless or with a very short coarse beak, 10-13-ribbed, as in *C. biennis*. In later years considerable variation was observed among the progenies of selfed plants of *C. artificialis*. As a result of testing selected individuals, Jenkins (unpublished) obtained new strains with various diploid chromosome numbers ranging from 20 to 36. Some of the new strains thus established appear to be fairly uniform morphologically. It is possible that in course of time several specific new types might be established, some of which would be capable of maintaining themselves in nature.

× *C. Bischoffi* Sch. Bip. in herb. "*C. rubro-foetida*" = *C. rubra* ($n=5$) × *C. foetida* ($n=5$). Seven sheets of specimens in Herb. Hort. Heidelb. ex herb. Sch. Bip. The plants are variable, some being more like *C. rubra* and others like *C. foetida*. (Cf. Poole, C. F., Univ. Calif. Publ. Agr. Sci. 6: 169-200. 1931; 231-255. 1932.)

× *C. curiensis* Bruegg., Jahresb. Naturf. Ges. Graub. 2(23-24): 110. 1880. *C. blattarioides* × *C. conyzaefolia* acc. to Churwalden, Fl. Cur. 70. 1868. Reported by Bruegger from Mittelberg in Vorarlberg, Switzerland in 1854. The following specimen has been seen: Croatia, Velebit Mts., *Borbas* (G ex herb. J. Ball). The leaves resemble those of *C. blattarioides*, but the involucre is more like that of *C. conyzaefolia*; flower head large, many-flowered; style branches yellow; achenes lacking.

× *C. Garnieri*, Petitmengin, Bull. Soc. Sci. Nancy ser. 3, 8(3): 213. 1906, *vide* Index Kewensis. When a search was made for this reference in the Bibliotheque De Lessert in 1925, it could not be found.

× *C. helvetica* Bruegg., Jahresb. Naturf. Ges. Graub. 2(23-24): 110. 1880. (× *C. oenipontana* J. Murr, Oest. Bot. Zeits. 43: 178. 1893; Deutsche Bot. Monatschr. 12: 19. 1894.) *C. blattarioides* × *C. alpestris* acc. to Churwalden, Fl. Cur. 70. 1868; *C. alpestris* × *blattarioides* acc. to J. Murr, *loc. cit.* Reported by Bruegger from 4 localities in Switzerland. The following specimen from Switzerland has been seen: Grisons, 1700-1780 m, *Thellung* (Ms, as Schinz n. 2246) as *C. helvetica*. This specimen bears the accompanying memorandum. "Hybrid tres polymorphe, formant a passage presque insensible de l'un parent a l'autre et dont il a été presque impossible de recueillir 20 exemplaires a peu pres semblables." In our cultivated hybrids between these two species the fertility was low; and the occurrence of such a hybrid swarm as the one observed by Thellung would necessitate the existence of at least several first generation hybrids. This could easily have occurred, however, since the two species will cross without difficulty. Out of 22 achenes produced by artificial crosses, we obtained 16 vigorous hybrids. The following specimens from Tirol have been seen: Innsbruck and Hall, 1100-1500 m, in calcareous gravel, very rare, *Murr* in 1895 (UWH), type of *C. oenipontana* Murr; Vorarlberg, *Murr* in 1908 (Bur).

After comparing Murr's type of $\times C. oenipontana$ with several specimens of *C. blattarioides*, the present author was inclined to consider Murr's plant as merely an extreme variant of the latter. Yet Huter (Oest. Bot. Zeits. 57: 112. 1907) lists, along with *C. oenipontana*, also *C. Peyritschii*, stating that it is more similar to *C. blattarioides* than is *C. oenipontana*. Therefore, it does not seem to the present author that *C. Peyritschii* should be recognized as a hybrid without supporting evidence.

$\times C. Holubyana$ Domin, Preslia (Ceskoslov. Bot. Spolec.) 13-15: 252, 1935. Czechoslovakia. *C. foetida rhoeadifolia* $\times C. setosa$ acc. to Holuby *vide* Domin (*loc. cit.*).

$\times C. hybrida$ A. Kern., Oest. Bot. Zeits. 20: 120. 1870. ($\times C. Muretiana$ Bruegg., Jahresb. Naturf. Ges. Graub. 2(23-24): 110. 1880.) *C. Jacquini* $\times C. terglouensis$, acc. to Bruegger (*loc. cit.*); A. Kerner, Sched. Fl. Exs. Austro-Hung. 1: 62. 1881; Fiori, Fl. Anal. Ital. 3(2): 438. 1904; Huter, Oest. Bot. Zeits. 57: 113. 1907. The following have been seen from central Tirol, Austria. Mt. Hühnerspiel, 2200-2400 m, Huter 1407 (UWH, G); Trins, Gschnitztal, near summit of the Blaser, 2250 m, with parent species, Churchill in 1873 (K, G); Mt. Blaser, Matreium, 2200 m, calcareous gravel, with parents, Obrist (G).

$\times C. Malyi$ Stadlmann, Oesterr. Bot. Zeits. 58: 425. 1908. *C. chondrilloides* $\times C. Blawii$, acc. to Stadlmann (*loc. cit.*). *C. Blawii* is *C. pannonica* m.v. 1 (see p. 442). The following have been seen: Istria, Carstiania, S. side of Mt. Lipnik and Kavce, 800 m, Justin in 1910 (UWG); S.W. Bosnia and Herzegovina, Tušnicagebiet, 1200-1300 m, Stadlmann in 1907 (UWG, UWH). A photograph of the latter is in Herb. Univ. Calif.

$\times C. longifolia$ Heer, ex Focke, Die Pflanzen-Mischlinge 215. 1881. *C. alpestris* $\times C. conyzaeifolia$, occurring in Switzerland, acc. to Focke (*loc. cit.*).

$\times pseudoblattarioides$ Borbas (cf. p. 301).

$\times C. turicensis$ Bruegg., Jahresb. Naturf. Ges. Graub. 2(23-24): 111. 1880. *C. biennis* $\times C. vesicaria taraxacifolia$, collected at Zurich in 1867-1868 acc. to Bruegger (*loc. cit.*).

SPECIES NOT SUFFICIENTLY KNOWN

Crepis Aitchisoni Boiss., Fl. Orient. Suppl. 324. 1888. (Fig. 305.) Perennial, 2.5–3.5 dm high; caudex vertical, 3–4 cm long, 0.5 cm wide, woody, covered with brown bases of old leaves, crowned with a rosette; leaves all caudical, pale green, glaucescent, pubescent on both sides with fine short gland hairs, 3–9 cm long, 1–2 cm wide, obovate to oblanceolate, acute or obtuse, lyrate-pinnatifid, terminal segment ovate to elliptic, lateral segments remote, triangular, acute, gradually reduced into a winged petiole with broader clasping base; stem erect, slender, terete, striate, glabrous, leafless except 2–4 small linear bracts, dichotomously branched near summit, 3–4-headed; peduncles 1.5–5.5 cm long, erect, slender, somewhat thickened, sulcate and pubescent near summit; heads erect, small, 30–40-flowered; involucre campanulate, in anthesis 9–10 mm high, about 5 mm wide at middle, densely pubescent with fine short yellow gland hairs; outer bracts 8–10, unequal, the longest about $\frac{1}{2}$ as long as the inner, lanceolate, acute, very dark; inner bracts 10–16, lanceolate, acute, paler toward base, glabrous on inner face; corolla 12–16 mm long; ligule 1.5 mm wide, pubescent on lower part and at summit of tube with very short trichomes; teeth about 0.7 mm long; corolla tube 3–5 mm long; anther tube 5×1.5 mm dis.; appendages 0.8 mm long, oblong, obtuse, constricted at base; style branches 2 mm long, 0.1 mm wide, yellow; achenes not seen; ovary 1 mm long, attenuate at summit; pappus white, 5–6 mm long, 1-seriate, nearly equally fine, rather stiff. Flowering June; flowers yellow. Known only from AFGHANISTAN: Hariab dist., in pine forests and in shelter of large rocks, 2575 m, *J. E. T. Aitchison* 48, June 25, 1880 (type Bo, K, G, DD), photograph of type sheet (UC, US, G, NY). *C. Aitchisoni* shows some resemblance to *C. bupleurifolia* of W. Armenia and Kurdistan in floral characters, especially in the constricted base of the anther appendages which has been seen in these species only. The involucre is also similar in the two species and the leaves of these species are also somewhat similar; but in habit and number of florets per head the plants differ considerably. Until more material of *C. Aitchisoni* is available, especially mature involucre and fruits, its classification must be postponed.

Crepis arenosa Scop., Annus I. Hist. Nat. 59. 1769.

Crepis ? *Bockiana* Diels, Engl. Bot. Jahrb. 29 : 633. 1901. Extract from translation of original description: "stem tall, remotely leafy, sparsely puberulent; leaves glabrous, several-pinnate, lobes subovate or lanceolate, margin slightly repand, minutely remotely denticulate, . . ." The rest of the original description applies only to a fragment bearing leaves and buds of *Youngia heterophylla* which is mounted together with another fragment on a sheet labeled *Crepis Bockiana* Diels sp. nov. ? This sheet is *Bock et v. Rosthorn 1593* (in Herb. Berol.), which is the only specimen cited in the original description. The second fragment, just mentioned is NOT *Youngia heterophylla*, if one may judge from a single leaf (there are no flowers or fruits). The leaf on this fragment, however, resembles the leaves on two other unidentified specimens, lacking flowers and fruits, in Herb. Berol., viz., *Bock et v. Rosthorn 871 ? and 987*. Both of these sheets have been annotated as follows: "*Zu Prenanthes* sp. ?" Not only are the leaves on these three specimens closely similar in shape; it happens also that they are all more or less infested with a leaf-spot fungus, whereas the leaves of the *Y. heterophylla* fragment on the "type sheet" are not so infested. This supports the evidence from leaf shape that the three collections, excluding the *Y. heterophylla* fragment, are all the same species. Furthermore, there can be no doubt that this species is distinct from all the known species of *Crepis* and *Youngia*.

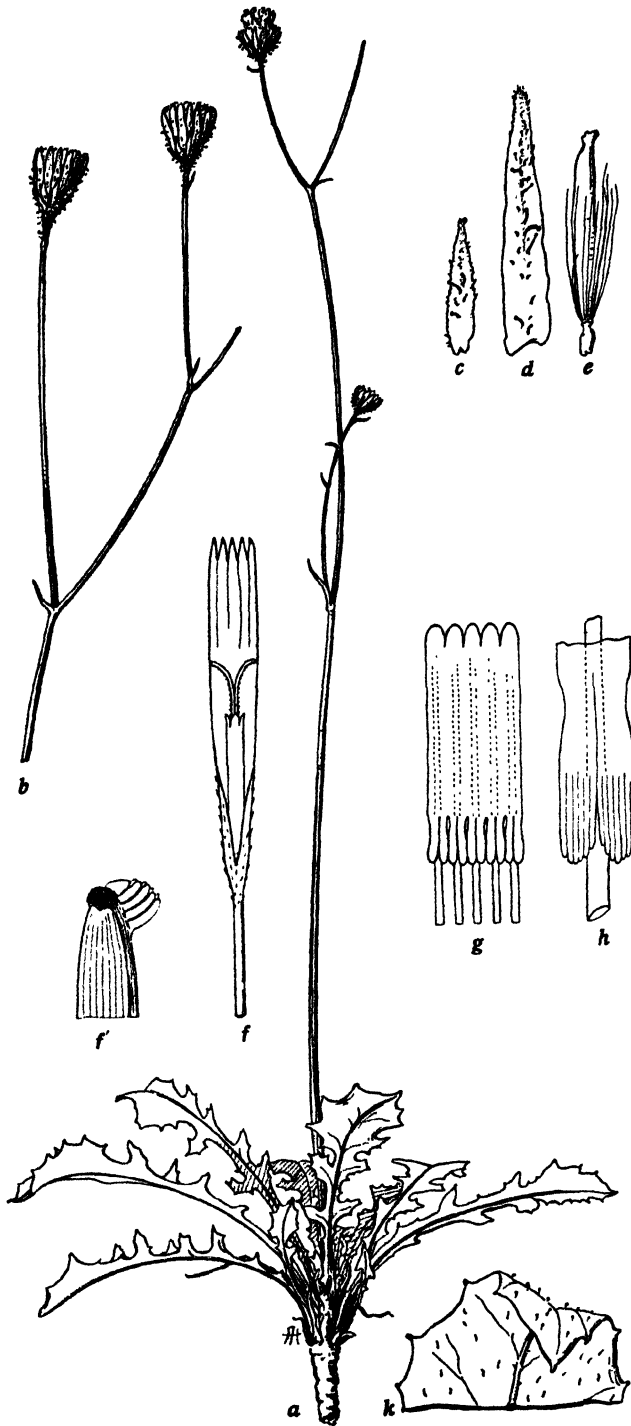


Fig. 305. *Crepis Aitchisoni*, from type (Bo) and isotype (G): a, plant, $\times \frac{1}{2}$; b, 2 young heads, $\times 1$; c, d, outer and inner involucre bracts, outer face, $\times 4$; e, young floret, $\times 4$; f, floret lacking ovary (a composite drawing from fragments), $\times 4$; f', detail of ligule tooth, $\times 25$; g, anther tube, $\times 8$; h, detail of appendages, $\times 32$; k, apex of leaf showing pubescence, $\times 2$.

Crepis calycina (Hoffm. et Lk.) Nym. Acc. to Cotinho (Fl. Port. 676. 1915), this is a dubious species not known in modern herbaria.

Crepis costata Candargy, Bull. Soc. Bot. Fr. 44: 147. 1897. Related to *C. pulchra* acc. to the author.

Crepis dubia Krock., Fl. Sil. 2(2): 324-6. 1773. Krock's herbarium was destroyed acc. to Handel-Mazzetti who, at my request, made inquiries at Breslau. It was suggested by its author that it might be a variety of *C. biennis*.

Crepis farinosa Lamk., Fl. Fr. 2: 112. 1778. Referred by its author to *C. tectorum* L., *C. virens* L., and *C. Dioscoridis* L.

Crepis glabra Krock., Fl. Sil. 4(2): 270. 1823. Compared by its author with *C. biennis* and *C. pulchra*. Krock's herbarium was destroyed acc. to Handel-Mazzetti.

Crepis glandulosa Bast., Desv. Jour. Bot. 3: 17. 1814; DC., Prod. 7: 172. 1838.

Crepis hastata Kit., Linnaea 32: 414. 1863. Perhaps = *C. capillaris*.

Crepis heterogyna Froel., ex DC., Prod. 7: 169. 1838. No spec. in herb. DC.

Crepis heterophylla Klatt, Annal. Naturh. Hofmus. Wien 9: 368. 1894. = *Hieracium*?

Crepis laevigata Dum., Fl. Belg. Prod. 61. 1827; DC., Prod. 7: 178. 1838 sub spp. non satis notae.

Crepis leiocarpa (Sch.) Steud., Nom. ed. 2, 437. 1840; *Gatyona leiocarpa* Sch., Flora 1839: 21.

Crepis Litardierei Emb., Bull. Soc. Sci. Nat. Maroc 15: 223. 1935. Known only from the original description, from which the affinities of the plant are not clear, even if it is to be accepted in *Crepis*.

Crepis nigrescens Pohle, Act. Hort. Jurjev. 3: 231. 1903. "Province Archangel." Probably *C. tectorum*.

Crepis paniculata Presl, Fl. Sic. 1: xxxi. 1826; DC., Prod. 7: 173. 1838; Guss., Fl. Sic. 2: 413. 1843.

Crepis pectinata Lowe, Trans. Camb. Phil. Soc. 4: 24. 1833. Probably *Tolpis*.

Crepis pulmonariaefolia Froel., ex DC., Prod. 7: 169. 1838. No spec. in herb. DC.

Crepis pungens Desf., ex DC., Prod. 7: 173. 1838. No spec. in herb. DC. Note in Herb. Berol. states "= *C. aculeata*."

Crepis ramosissima Kit., Linnaea 32: 414. 1863.

Crepis ramosissima Spreng., Syst. 3: 634. 1826.

Crepis ramosissima Urv., Mem. Soc. Linn. Paris 1: 102. 1822; DC., Prod. 7: 162. 1838; Ledeb., Fl. Ros. 2: 822. 1844-1846. No spec. in Herb. Paris, nor in herb. DC. In Ledeb. (*loc. cit.*) it follows *C. parviflora*.

Crepis reflexa Guss., Fl. Sic. 2: 413. 1843. Related to *C. vesicaria* acc. to author.

Crepis (*Barkhausia*) *repens* Spreng., Syst. 3: 652. 1826; Hook. et Arn., Bot. Beech. 1: 194. 1834 (?); DC., Prod. 7: 159. 1838. *Ixeris*?

Crepis (*Barkhausia*) *Roylei* (DC.) F. W. Sch., Flora 23: 718. 1840; DC., Prod. 7: 157. 1838. If a specimen exists in herb. DC., it was not seen by me. Hooker (Fl. Brit. Ind. 3: 399. 1882, under *Pterotheca Falconeri*) states that de Candolle's description is not sufficient to identify the plant, which is true; also, that there is no spec. of *P. Falconeri* in Royle's herbarium. The other species which was transferred by Clarke (256) to *Pterotheca bifida* is *Barkhausia porrifolia* DC., which is presumably a species of *Ixeris*.

Crepis sagittata Schur, Verh. Naturf. Ver. Brünn 36: 213-14. 1897.

Crepis sagittata Wender., Ind. Sem. Hort. Marb. 1819; Linnaea 5: Litt. 54. 1830; DC., Prod. 7: 173. 1838. No spec. in herb. DC.

Crepis scepusiensis Kit., Linnaea 32: 413. 1863.

Crepis Schreberi Froel., ex DC., Prod. 7 : 168. 1838. No spec. in herb. Schreb. at Munich ; no information available at Göttingen ; no spec. in herb. DC.

Crepis sicula Ucria, Roem. Arch. Bot. 1(1) : 69. 1796.

Crepis silenifolia Froel., ex DC., Prod. 7 : 169. 1838. No spec. in herb. DC.

Crepis spinosissima Bellardi, ex Colla, Herb. Pedem. 3 : 500. 1834 in obs.

Crepis sulphurea Pourr., ex Willk. et Lange, Prod. Fl. Hisp. 2 : 251. 1870 sub species dubiae.

Crepis Vandasii Rohl., Sitz. Ges. Wissensch. Vestnik 38 : 66. 1904. No spec. seen. From the description, possibly a distinct species. A spec. in herb. Burnat, labeled *C. Baldaccii* Hal., *Baldacci* n. 144 in 1894, Mt. Cika, may be this.

Crepis variabilis Krock., Fl. Sil. 2 : 326. 1793. Krock's herb. was destroyed.

EXCLUDED NAMES

NOTE.—In all the references to Index Kewensis (I.K.) it will be understood that Hooker f. and Jackson are the authors.

- Crepis abietina* Boiss. et Bal., ex Boiss., Fl. Or. 3: 803. 1875.—*Mulgedium abietinum* fide I.K.; nom. nud. ?
- C. abolini* Popov, ex Pavlov, Bull. Soc. Nat. Mosc. n.s., 42: 128. 1933, nom. nud. fide I.K.
- C. acaulis* Hook. f., Fl. Brit. Ind. 3: 396. 1882.—*Launaea acaulis* (Roxb.) Babc., ex Craib, Fl. Siam. Enum. 2: 299. 1936.
- C. altissima* Balb., Cat. Hort. Taur. 15. 1804.—*Tolpis virgata* fide I.K.
- C. ambacensis* Hiern., Cat. Welw. Afr. Pl. 3: 618. 1898.—*Lactuca* fide Stebbins ined.
- C. ambigua* Balb., Mem. Acad. Turin 14(2): 69. 1805.—*Tolpis virgata* fide I.K.
- C. ambigua* A. Gray, Pl. Fendl. 114. 1849.—*Hieracium Fendleri* Sch. Bip., Bonplandia 9: 173. 1861.
- C. ambigua* A. Gray, Pl. Wright, 1: 129. 1852.—*Hieracium Wrightii* Robins. et Greenm., Proc. Am. Acad. n.s., 28: 19. 1904.
- C. Apargia* Pers., Syn. 2: 375. 1808.—*Chondrilla Peltidium* fide I.K.
- C. apargioides* Willd., Sp. Pl. 3: 1594. 1804.—*Chondrilla Peltidium* fide I.K.
- C. aspera* Lamm., Encyc. 2: 180. 1786.—*Picris aspera* fide I.K.
- C. atripappa* Babc., Univ. Calif. Publ. Bot. 14: 324. 1928.—*Youngia gracilis* in Babc. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 67. 1937.
- C. baetica* Mill., Gard. Dict. ed. 8, no. 3.—*Tolpis barbata* fide I.K.
- C. baicalensis* Ledeb., Mem. Acad. Petersb. 5: 559. 1812.—*Youngia tenuifolia* subsp. *typica* Babc. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 48. 1937.
- C. barbata* L., Sp. Pl. 805. 1753.—*Tolpis barbata*, spec. in Herb. Linn.
- C. bhotanica* Hutchinson, Kew Bull. 1916: 189.—*Dubyaea hispida* (Don) DC., Prod. 7: 247. 1838; Stebbins, Mem. Torr. Bot. Club 19: 19. 1940.
- C. Blinii* Lévl., Fedde Rep. 13: 345. 1914; Bull. Geogr. Bot. 25: 15. 1915.—*Hieracium!* Type Spec. in herb. De Lessert.
- C. Boliviensis* Wedd., Chlor. And. 1: 226. t. 42A. 1857.—*Hieracium boliviense* Sch. Bip., Bonplandia 9: 173–4. 1861.
- C. Bonii* Gagnep., Bull. Soc. Bot. Fr. 68: 47. 1921.—*Ixeris!*
- C. borealis* Sch. Bip., in Walp., Rep. 2: 698. 1843.—*Leontodon borealis* fide I.K.
- C. bracteolata* Fries, Epier. 71. 1862.—*Hieracium* fide Zahn.
- C. bulbosa* Tausch, Flora 11 (I Erg.): 78. 1828.—*Actheorrhiza bulbosa* (L.) Cass., Dict. 48: 425. 1827; Babc. et Stebbins, Univ. Calif. Publ. Bot. 18: 235. 1943.
- C. canariensis* Grande, Bull. Orto Bot. Napoli 4: 170. 1914, nom. nud. fide I.K.
- C. Candeli* Sennen, Bull. Soc. Bot. Fr. 78: 187. 1931, nomen, fide I.K.
- C. (Barkhausia) chaetocephala* Bge., Fl. Russlands [alias Lehman, A. Reliq. Bot.] in Mem. Acad. Petersb. Sav. Etr. 7: 384 (208). 1851.—Type could not be found at Paris fide H. M. Hall. Probably *Heteroderis*.
- C. Chanetii* Lévl., Fedde Rep. 11: 306. 1912.—Type in Herb. Edinburgh; involucre consists of 1 series of bracts; achenes prismatic; not *Crepis!*
- C. Charbonnelii* Lévl., Fedde Rep. 12: 100. 1913.—*Lactuca tatarica* (L.) C. A. Mey., fide Handel-Mazzetti, Acta Hort. Gothol. 12: 352. 1938.
- C. cichorioides* Hiern., Cat. Welw. Afr. Pl. 1: 617. 1898.—*Lactuca!* fide Stebbins ined.
- C. cineripappa* Babc., Univ. Calif. Publ. Bot. 14: 325. 1928.—*Youngia cineripappa* (Babc.) Babc. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 62. 1937.

- C. coriacea* Hornem., Hort. Hafn. 2: 768. 1813; DC., Prod. 7: 172. 1838.—No. spec. in herb. DC. Isotype in Herb. Hauiensis (C) is certainly *Tolpis*!
- C. coronopifolia* Desf., Act. Soc. Hist. Nat. Par. 1: 38. 1792.—Spec. in herb. Willd. (B) no. 14760 = *Tolpis*!
- C. coronopus* Gagn., Bull. Soc. Bot. Fr. 68: 48. 1921.—*Ixeris*!
- C. crinita* Soland, ex Lowe, Trans. Camb. Phil. Soc. 4: 24. 1831.—*Tolpis crinita* fide I.K.
- C. crithmifolia* Link, ex Buch, Besch. Canar. Ins. 147. 1819.—*Tolpis crithmifolia* fide I.K.
- C. dentata* Sch. Bip., ex Zoll., Syst. Verz. Ind. Archip. 126. 1854.—*Ixeris denticulata* (Houtt.) Stebbins. See specimen of Zollinger no. 249 in herb. Cosson (PC).
- C. depressa* Hook. f. et Thoms., Fl. Brit. Ind. 3: 397. 1882.—*Youngia depressa* (Hook. f. et Thoms.) Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 33. 1937.
- C. disciformis* Mattf., Notizbl. Bot. Gart. Berlin 12: 685. 1935.—*Lactuca disciformis* (Mattf.) Stebbins, Mem. Torrey Bot. Club 19: 50. 1940.
- C. distincta* Popov et Vved., Bull. Soc. Nat. Mosc. n.s., 42: 128, 147. 1933.—*Youngia distincta* (Popov et Vved.) Bab. et Stebbins, Univ. Calif. Publ. Bot. 18: 233. 1943.
- C. diversifolia* Ledeb., ex Spreng., Syst. 3: 657. 1826.—*Youngia tenuifolia diversifolia* (Ledeb.) Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 54. 1937.
- C. dubyaca* (Clarke) Marq. et Shaw, Jour. Linn. Soc. 48: 194. 1929.—*Dubyaea hispida* (Don) DC., Prod. 7: 247. 1838; Stebbins, Mem. Torr. Bot. Club 19: 19. 1940.
- C. dumicola* Hiern., Cat. Welw. Afr. Pl. 3: 618. 1898.—*Lactuca dumicola* S. Moore, Jour. Bot. 65 (Suppl. 2): 67. 1927, fide Stebbins.
- C. echinoides* All., Fl. Pedem. 1: 222. 1785.—*Helminthia echinoides* fide I.K.
- C. elegans* Fisch., ex DC., Prod. 7: 161. 1838.—*C. baicalensis* fide I.K. = *Youngia tenuifolia* subsp. *typica* Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 48. 1937, fide I.K.
- C. ephemera* Hiern., Cat. Welw. Afr. Pl. 1: 616. 1898.—Type in Herb. Brit. Mus. = *Tolpis ephemera* (Hiern.) Stebbins ined.
- C. ephemeroides* S. Moore, Jour. Bot. 54: 286. 1916.—Type in Herb. Brit. Mus. = either *Hieracium* or *Tolpis*, probably *Tolpis ephemera*.
- C. fastigiata* Sch. Bip., ex Zoll., Syst. Verz. Ind. Archip. 125. 1854.—*C. japonica* Benth., fide I.K. = *Youngia japonica* (L.) DC., Prod. 7: 194. 1838; Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 94. 1937.
- C. filiformis* Dryand., ex Ait., Hort. Kew ed. 1, 3: 128. 1789; Willd., Sp. Pl. 3: 1607. 1804; Pers. Syn. Pl. 2: 377. 1807.—*Tolpis*! fide Horwood (Herb. Kew.).
- C. flexuosa* Bernh., ex Steud., Nom. ed. 2, 1: 436. 1840–1841.—*Sonchus flexuosus* fide I.K.
- C. foetens* Froel., ex DC., Prod. 7: 172. 1838; *Hieracium foetidum* Willd., Sp. Pl. 3: 1575. 1804; *Hieraciodes foetens* O. Kuntze, Gen. 1: 346. 1891.—Type in herb. Willd. (B) no. 14676 = *Taraxacum*! fide Mattfeld. Note.—The spec. of de Tournefort from Galatia in Herb. Paris (ex herb. Vaillant) labeled "H. Dentis-Leonis etc.," is apparently a different species of *Taraxacum*.
- C. formosana* Hayata, Jour. Coll. Sci. Tokyo 30: 163. 1911.—*Youngia japonica* (L.) DC. subsp. *genuina* (Hochr.) Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 95. 1937, ex descr.
- C. fusca* Bab., Univ. Calif. Publ. Bot. 14: 327. 1928.—*Youngia fusca* (Bab.) Bab. et Stebbins. *op. cit.* 77.

- C. fuscipappa* Benth. et Hook. f., Gen. Pl. 2(1) : 254. 1873; C. B. Clarke, Comp. Ind. 254. 1876.—*Youngia fuscipappa* Thwaites, Enum. Pl. Zeyl. 168. 1864; Babe. et Stebbins, *op. cit.* 65.
- C. Fussii* Kovata, ex Janka, Linnaea 30 : 587. 1859–1860.—*Hieracium rotundatum* fide I.K.
- C. Geisseana* Phil., Anal. Univ. Chil. 87 : 328. 1894.—*Malacothrix obtusa* Benth., fide O. Hoffm.
- C. Gillii* S. Moore, Jour. Bot. 47 : 170. 1899.—*Soroseris Gillii* subsp. *typica* Stebbins, Mem. Torrey Bot. Club 19 : 42. 1940.
- C. Gillii* var. *hirsuta* Anthony, Notes Bot. Gard. Edinb. 18 : 193. 1934.—*Soroseris Gillii* subsp. *hirsuta* (Anthony) Stebbins, *op. cit.* 44.
- C. Gillii* var. *bellidifolia* Hand.-Mazz., Acta Hort. Gothob. 12 : 355. 1938.—*Soroseris bellidifolia* (Hand.-Mazz.) Stebbins, *op. cit.* 38.
- C. Gillii* var. *erysimoides* Hand.-Mazz., Acta Hort. Gothob. 12 : 35. 1938.—*Soroseris Hookeriana* subsp. *erysimoides* Stebbins, *op. cit.* 46.
- C. glomerata* Benth. et Hook. f., Gen. Pl. 2(1) : 515. 1873; Hook. f., Fl. Brit. Ind. 2 : 398. 1882 p.p.—*Soroseris glomerata* (Dcne.) Stebbins, Mem. Torr. Bot. Club 19 : 35. 1940.
- C. glomerata* Hook. f., Fl. Brit. Ind. 3 : 398. 1882 p.p.—*Soroseris Deasyi* (S. Moore) Stebbins, *op. cit.* 36; *S. pumila* Stebbins, *op. cit.* 40; *S. Gillii* subsp. *occidentalis* Stebbins, *op. cit.* 44; *S. Hookeriana* subsp. *typica* Stebbins, *op. cit.* 45.
- C. glomerata* Clarke, Comp. Ind. 255. 1876.—*Soroseris depressa* (Hook. f. et Thoms., *loc. cit.*) Stebbins (*loc. cit.*).
- C. glomerata* var. *porphyrea* Marq. et Shaw, Jour. Linn. Soc. Bot. 48 : 194. 1929.—*Lactuca porphyrea* Stebbins, *op. cit.* 49.
- C. gracilipes* Hook. f., Fl. Brit. Ind. 3 : 396. 1882.—*Youngia depressa* Babe. et Stebbins, Carnegie Inst. Wash. Publ. No. 484 : 42. 1937.
- C. gracilis* Hook. f. et Thoms., ex C. B. Clarke, Comp. Ind. 254. 1876.—*Youngia gracilis* Hook. f., ex Babe. et Stebbins, *op. cit.* 67.
- C. graminifolia* Ledeb., Mem. Acad. Petersb. 5 : 558. 1814.—*Ixeris graminea* Nakai, Tokyo Bot. Mag. 36 : 23. 1922.
- C. Hallii* Sennen, Bull. Soc. Bot. Fr. 74 : 385. 1927, nom. nud.
- C. Henryi* Diels, Engl. Bot. Jahrb. 29 : 633. 1901.—*Youngia Henryi* (Diels) Babe. et Stebbins, Carnegie Inst. Wash. Publ. No. 484 : 85. 1937.
- C. heterantha* Sch. Bip., Pollichia 32–34 : 318. 1866.—*Lactuca Dubyaea* fide I.K. = *Dubyaea hispida* (Don) DC., Prod. 7 : 247. 1838; Stebbins, Mem. Torrey Bot. Club 19 : 19. 1940.
- C. heterogyna* Froel., ex DC., Prod. 7 : 169. 1838.—*Hieracium stuppeum* fide Zahn.
- C. heterophylla* Hemsl., Jour. Linn. Soc. 23 : 475. 1888.—*Youngia heterophylla* Babe. et Stebbins, Carnegie Inst. Wash. Publ. No. 484 : 88. 1937.
- C. hieracioides* Lamk., Fl. Fr. 2 : 111. 1792.—*Picris hieracioides* fide I.K.
- C. hieracioides* Schrank, Baier Fl. 2 : 338. 1789.—*Picris laciniata* fide I.K.
- C. Hieracium* Lévl., Fedde Repert. 13 : 345. 1914.—Type could not be found at Edinburgh. *Hieracium* ? *Youngia* ?
- C. hirta* L., Sp. Pl. 807. 1753.—*Leontodon hirtus* fide I.K.
- C. hispidissima* Bartl., ex Bartl. et Wendl. f., Beitr. 2 : 125. 1825; Rechb., Fl. Germ. Exc. 258. 1830–1832.—*Picris laciniata* fide I.K.
- C. hispidula* Delile, Fl. Egypte 261. t. 42. 1813.—*Leontodon hispidulus* fide I.K.
- C. Hookeriana* C. B. Clarke, Comp. Ind. 255. 1876.—*Soroseris Hookeriana* subsp. *typica* Stebbins, Mem. Torrey Bot. Club 19 : 45. 1940.
- C. incana* Lapeyr., Hist. Abr. Pl. Pyr. 483. 1813.—*Andryala integrifolia* fide I.K.

- C. incrassata* Banks, ex Lowe, Trans. Camb. Phil. Soc. 4: 24. 1831.—*Tolpis crinita* fide I.K.
- C. integra* Miq., Ann. Mus. Bot. Lugd. 2: 190. 1865–1866.—*Ixeris lanceolata* (Houtt.) Stebbins, Jour. Bot. 75: 46. 1937.
- C. integra* (non Miq.) Hayata, Jour. Sci. Imp. Univ. Tokyo 17(8): 38. 1904; Matsumura et Hayata, *op. cit.* 22: 211. 1906.—*Ixeris koshunensis* (Hayata) Stebbins, Jour. Bot. 75: 45. 1937.
- C. integra* (non Miq.) Hayata, Icon, Pl. Form. 8: 79. 1918.—*Ixeris taiwaniana* (Nakai) Stebbins, Jour. Bot. 75: 46. 1937.
- C. integra* (non Miq.) var. *pinnatiloba* Maxim., Mém. Biôl. 9: 350. 1874.—*Crepidiastrum lanceolatum* f. *pinnatilobum* (Maxim.) Nakai, *op. cit.* 151; *Ixeris* Stebbins (loc. cit.).
- C. japonica* Benth., Fl. Hongk. 194. 1861.—*Youngia japonica* (L.) DC. subsp. *genuina* (Hochr.) Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 95. 1937.
- C. japonica* var. *genuina* et var. *Elstonii* Hochr., Candollea 5: 340. 1931–1934.—*Youngia japonica* (L.) DC., subsp. *genuina* et subsp. *Elstonii* Bab. et Stebbins, *op. cit.* 95, 98.
- C. Keiskeana* Maxim., Bull. Acad. St. Petersb. 19: 523. 1874.—*Ixeris Keiskeana* (Maxim.) Stebbins, Jour. Bot. 75: 46. 1937.
- C. kikitatensis* Suksd., ex Piper, Bull. Torrey Bot. Club 1901: 43, nom. nud.
- C. koshunensis* Hayata, Ic. Pl. Form. 8: 79. t. 32. 1918.—*Ixeris koshunensis* (Hayata) Stebbins, Jour. Bot. 76: 45. 1937.
- C. laciniata* Schkuhr, ex DC., Prod. 7: 129. 1838.—*Picris laciniata* fide I.K.
- C. laevigata* Sch. Bip., ex Zoll., Syst. Verz. Ind. Archip. 125. 1854.—Type in herb. Cosson (P) = *Ixeris laevigata* (Blume) Stebbins, Jour. Bot. 75: 50. 1937.
- C. lanceolata* var. *platyphylla* Makino, Bot. Mag. Tokyo 17: 88. 1903.—*Ixeris lanceolata* subsp. *platyphylla* (Makino) Stebbins, Jour. Bot. 75: 46. 1937.
- C. lanceolata* var. *pinnatiloba* Makino, Bot. Mag. Tokyo 17: 88. 1903.—*Crepidiastrum lanceolatum* f. *pinnatilobum* (Maxim.) Nakai, *op. cit.* 151.
- C. lanceolata* Sch. Bip., ex Zoll., Syst. Verz. Ind. Archip. 126. 1854.—*Crepidiastrum lanceolatum* Nakai, *op. cit.* 150; nomen, fide I.K.
- C. lappacea* Host, Fl. Austr. 2: 421. 1831.—*Picris laciniata* fide I.K.
- C. lappacea* Lapeyr., Hist. Abr. Pl. Pyr. 483. 1813.—*Picris hieracioides* fide I.K.
- C. lappacea* Willd., Sp. Pl. 3: 1599. 1804.—*Picris pauciflora* fide I.K.
- C. Lechleri* Sch. Bip., ex Lechler, Berb. Am. Austr. 54. 1857.—Type in Herb. Berol. = *Troximon*!
- C. (Barkhausia) leucocephala* Bge., Fl. Russlands [alias Lehman, A., Reliq. Bot.] in Mem. Acad. Petersb. Sav. Etr. 7: 385. 1851.—*Heteroderis*?
- C. linguaeifolia* Maxim., Mém. Biôl. 9: 351. 1874; Bull. Acad. Petersb. 19: 525. 1874.—*Crepidiastrum linguaeifolium* (A. Gray) Nakai, Bot. Mag. Tokyo 34: 152. 1920.
- C. longipes* Hemsl., Jour. Linn. Soc. 23: 476. 1888.—*Youngia longipes* (Hemsl.) Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 94. 1937.
- C. Lowei* Sch. Bip., ex Webb et Berth., Phyt. Canar. 3: 461. 1836–1850, nomen.—The name was intended to include both *C. canariensis* (Sch. Bip.) Bab. and *C. vesicaria* subsp. *andryaloides* (Lowe) Bab.
- C. lyrata* Benth. et Hook. f., Gen. 2: 514. 1873; C. B. Clarke, Comp. Ind. 253. 1876.—*Youngia japonica* (L.) DC. subsp. *genuina* (Hochr.) Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 95. 1937.
- C. macrorrhiza* Banks, ex Hook., Bot. Mag. n.s. 4: t. 2988.—*Tolpis macrorrhiza* fide I.K.

- C. Mairei* Lévl., Fedde Repert. 12: 531. 1913.—*Youngia Mairei* (Lévl.) Bab. et Stebbins, *op. cit.* 79.
- C. Marschalliana* Rehb., Ic. Fl. Germ. 19: 126. 1834–1870, sphalm. vide *Crepinia Marschalliana* fide I.K. = *C. sancta bifida*.
- C. (Barkhausia) melanocephala* Bge., Fl. Russlands [alias Lehman, A., Reliq. Bot.] in Mem. Acad. Petersb. Sav. Etr. 7: 385. 1851.—*Heteroderis* ?
- C. microcephala* C. B. Clarke, ex Hook. f., Fl. Brit. Ind. 3: 415. 1882.—*Launaca microcephala* fide I.K.
- C. mauritiana* (Willd.) Froel., ex DC., Prod. 7: 164. 1838.—*Hieracium mauritianum* Willd. = *Reichardia* ?
- C. molokaiensis* Lévl., Fedde Repert. 10: 122. 1911.—Type in Herb. Paris = *Hypochaeris glabra* L.
- C. montana* Bernh., Syst. Verz. Erf. 138. 1800.—*Hieracium sabaudum* fide I.K.
- C. nana* Sch. Bip., Flora 1852: 48, non Richard.—*Crepidiastrum lanceolatum* (Houtt.) Nakai, Bot. Mag. Tokyo 34: 150. 1920.
- C. nemorosa* Less., Linnæa 9: 157. 1834, nomen, fide I.K.
- C. nivalis* Sch. Bip., ex Schweinf. et Aschers., in Schweinf., Fl. Aethiop. 284. 1867.—Authentic spec. of Schimper collected Oct. 7, 1850, Mt. Dedschen, Abyssinia, 13,500 ft., in Herb. Paris, is mounted on same sheet with *Dianthocercis Schimper* Sch. Bip. and is that species.
- C. novae-zelandiae* Hook. f., Handb. New Zeal. Fl. 164. 1864.—Type in Herb. Kew = *Launaca* fide Stebbins.
- C. nudicaulis* L., Sp. Pl. 805. 1753.—Non *Crepis*! *Lcontodon Villarsii* Lois., vel nomen confusum, fide Lacaita, Jour. Bot. 56: 97. 1918.
- C. nudicaulis* Sch. Bip., MS. in Zoll., Syst. Verz. Ind. Archip. 125. 1854.—*Ixeris pygmaea* (Zoll. et Mor.) Stebbins, Jour. Bot. 75: 50. 1937.
- C. nutans* Geyer, ex Hook., Lond. Jour. Bot. 6: 253. 1847.—*Calais nutans* fide I.K.
- C. (Paleyia) oligocephala* Sch. Bip., Pollichia 2: 320. 1866.—*Dubyaea oligocephala* (Sch. Bip.) Stebbins, Mem. Torrey Bot. Club 19: 22. 1940.
- C. oligophylla* Klatt, ex Schinz, Bull. Herb. Boiss. 3: 426. 1895.—Type in Herb. Bot. Mus. Univ. Zurich = *Lactuca* fide O. Hoffmann in herb.
- C. paleacea* Diels, Notes Roy. Bot. Gard. Edinb. 25: 202. 1912.—*Youngia paleacea* subsp. *typica* Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 68. 1937.
- C. pallida* Hort. Par., ex Sch. Bip., in Webb et Berth., Phyt. Canar. 2: 400. 1836–1850.—*Tolpis barbata* fide I.K.
- C. pannonica* Stadl., Oesterr. Bot. Zeitschr. 56: 271. 1906, nomen, fide I.K.
- C. papuana* S. Moore, Trans. Linn. Soc. Bot. 9: 87. 1916.—*Ixeris papuana* (S. Moore) Stebbins, Jour. Bot. 75: 50. 1937.
- C. pectinata* Steph., ex Herd., Bull. Soc. Nat. Mosc. 43: 197. 1870.—*C. tenuifolia* fide I.K. (cf. *Youngia*).
- C. pinnatifida* Fröl., ex DC., Prod. 7: 167. 1838; Willd., ex Boiss., Fl. Orient. 3: 840. 1875.—*Taraxacum* ex descr.
- C. pinnatifida* Hort., ex DC., Prod. 7: 93. 1838.—*Hypochaeris pratensis* fide I.K.
- C. Poeppigii* Sch. Bip., Flora 38: 122. 1855.—*Troximon Lechleri* (cf. *C. Lechleri*).
- C. polycephala* Sch. Bip., ex Zoll., Syst. Verz. Ind. Archip. 126. 1854, nomen, fide I.K.
- C. porrifolia* Don, Prod. Fl. Nep. 164. 1825.—*Ixeris* ? fide Stebbins.
- C. Pratti* Bab., Univ. Calif. Publ. Bot. 14: 331. 1928.—*Youngia Pratti* (Bab.) Bab. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 81. 1937.
- C. prenanthoides* Hemsl., Jour. Linn. Soc. Bot. 13: 477. 1888.—*Lactuca chunkingensis* Stebbins, Jour. Bot. 75: 15. 1937.

- C. primulifolia* Hook. f., ex Benth. et Hook. f., Gen. Pl. 2(1): 514. 1873; C. B. Clarke, Comp. Ind. 257. 1876.—*Youngia cineripappa* (Babc.) Babc. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 62. 1937.
- C. pseudovirens* Lévl., Fedde Repert. 11: 306. 1912.—*Ixeris*!
- C. (Aracium) pubescens* C. Koch, Linnaea 23: 681. 1850.—Spec. in Herb. Berol. = *Hieracium*!
- C. pulcherrima* Fisch., ex Link, Enum. Hort. Berol. 2: 290. 1822.—Authentic spec. of Fischer in herb. De Lessert = *Youngia tenuifolia* subsp. *typica* Babc. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 48–49. 1937.
- C. pungens* Desf., Tabl. ed. 1. 88. 1804, nomen fide I.K.
- C. racemifera* Hook. f., Fl. Brit. Ind. 3: 397. 1882.—*Youngia racemifera* (Hook. f.) Babc. et Stebbins, Univ. Calif. Publ. Bot. 18: 229. 1943.
- C. radicata* Forsk., Fl. Aeg.-Arab., 145. 1775.—An authentic spec. of Forskål in Herb. Huiensis (C), which, acc. to Carl Christensen (*in litt.*), agrees better with Forskål's desc. of *C. radicata* than with any other plant mentioned or described by him, was identified as *Picris coronopifolia* DC. by Christensen.
- C. rapunculoides* Dunn, Jour. Linn. Soc. 35: 512. 1901–1904.—*Youngia racemifera* (Hook. f.) Babc. et Stebbins, *loc. cit.*
- C. rhagadioloides* L., Mant. 108. 1767.—*Picris Sprengeriana* fide I.K.
- C. rifana* Maire et Sennen, ex Sennen et Maur., Cat. Fl. Rif. Or. 73. 1933, nomen fide I.K.
- C. rigens* Dryand., ex Ait., Hort. Kew. Cat. 3: 127. 1789.—Authentic spec. in Herb. Brit. Mus., acc. to A. B. Rendle (*in litt.*), is *Microderis rigens* DC., which is referred to *Picris* by Bentham (Gen. Pl. 2 [1]: 512. 1873–1876) and to *Leontodon* by O. Hoffm. (Pflanzenfam. 4[5]: 363. 1891).
- C. Rosthornii* Diels, Engl. Bot. Jahr. 29: 632. 1901.—*Youngia Rosthornii* (Diels) Babc. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 92. 1937.
- C. rosularis* Diels, Notes Roy. Bot. Gard. Edinb. 25: 201. 1912.—*Soroseris rosularis* (Diels) Stebbins, Mem. Torr. Bot. Club 19: 37. 1940.
- C. rupestris* Rehb., ex Moessl., Handb. ed. 2, 2: 1402. 1827–1829.—*Hieracium rupestre* fide I.K.
- C. scabra* Lapeyr., Hist. Abr. Pl. Pyr. 483. 1813.—*Picris hieracioides* fide I.K.
- C. scaposa* Chang, Sinensia 3: 201. 1933.—*Youngia scaposa* (Chang) Babc. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 46. 1937.
- C. setgetum* Schleich., Cat. Pl. Helv. ed. 4, 14. 1821, nomen, fide I.K.
- C. scrawschanica* B. Fedtsch., Beih. Bot. Centralbl. 40: 203. 1923.—*Youngia seraw-schanica* (B. Fedtsch.) Babc. et Stebbins, Univ. Calif. Publ. Bot. 18: 231. 1943.
- C. setigera* Scott ex W. W. Smith, Notes Bot. Gard. Edinb. 8: 333. 1915.—*Youngia setigera* (Scott) Babc. et Stebbins, Univ. Calif. Publ. Bot. 18: 227. 1943.
- C. sibirica* C. B. Clarke, Comp. Ind. 252. 1876; Hook. f., Fl. Brit. Ind. 3: 394. 1882, non L.—*Dubyaea oligocephala* (Sch. Bip.) Stebbins, Mem. Torrey Bot. Club 19: 20. 1940.
- C. silhetensis* Hook. f., Fl. Brit. Ind. 3: 397. 1882.—*Youngia silhetensis* (DC.) Babc. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 104. 1937.
- C. simplex* Froel., ex DC., Prod. 7: 168. 1838.—Authentic spec. of Viviani in Herb. Libyc. (Genoa) = *Hieracium simplex* Viv., Fl. Libyc. Spec. 50. t. 13 f. 4. 1824. = *Leontodon Salzmannii* fide I.K.
- C. simulatrix* Babc., Univ. Calif. Publ. Bot. 14: 329. 1928.—*Youngia simulatrix* (Babc.) Babc. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 40. 1937.
- C. sinuata* Lamk., Encyc. 2: 179. 1786.—*Picris asplenioides* fide I.K.
- C. Sodiroi* Hieron., ex Sod., Engl. Bot. Jahrb. 29: 84. 1900–1901.—*Hieracium*!

- C. sorocephata* Hemsl., Jour. Linn. Soc. 30: 116. t. 4. f. 1-4. 1894.—*Sorosseris glomerata* (Dcne.) Stebbins, Mem. Torrey Bot. Club 19: 35. 1940.
- C. Sprengeriana* Willd., Sp. Pl. 3: 1598. 1804; Ait., Hort. Kew. Cat. ed. 2, 4: 456-461. 1812.—*Picris Sprengeriana* fide I.K.
- C. Sprengeriana* All., Fl. Pedem. 1: 221. 1785.—*Picris pauciflora* fide I.K.
- C. stenoma* Turcz., ex DC., Prod. 7: 164. 1838.—*Youngia stenoma* (Turcz.) Ledeb., Fl. Ros. 837. 1844-1846; Babc. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 44. 1937.
- C. stenothea* Fries, ex Walp., Ann. 2: 1009. 1851-1852.—*Hieracium Crepidispermum* fide I.K.
- C. Stocksiana* Aitch. et Hemsl., ex Aitch., Trans. Linn. Soc. ser. 2, 3: 82. 1888.—Authentic spec. in Herb. (K, DD, Fl, G) are all *Heteroderis*!
- C. stolonifera* Lévl., Fedde Repert. 12: 531. 1913, non *Ixeris stolonifera* A. Gray.—*Lactuca Stebbinsiana* Hand.-Mazz., Acta Hort. Gothob. 12: 353. 1938.
- C. striata* Thunb., Prod. Pl. Cap. 139. 1772-1775.—*Hieracium capense* fide I.K.
- C. suaveolens* Hort., ex Colla, Herb. Pedem. 3: 500. 1834. nomen ?
- C. succulenta* Dryand., ex Ait., Hort. Kew. Cat. ed. 1, 3: 128. 1789.—*Tolpis fruticosa* fide I.K.
- C. szechuanica* Söderb., Svensk Bot. Tidskr. 28: 362. 1934, nomen, fide I.K.
- C. tanegana* Miq., Ann. Mus. Bot. Lugd. 3: 298. 1867.—*Crepidiastrum lanceolatum* (Houtt.) Nakai, Bot. Mag. Tokyo 34: 150. 1920.
- C. Taquetii* Lévl. et Vant., Fedde Repert. 8: 140. 1910.—*Youngia japonica* subsp. *genuina* Babc. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 95. 1937.
- C. Taraxacum* Stokes, ex With., Bot. Arr. ed. 2, 2: 853. 1787-1793.—*Taraxacum officinale* fide I.K.
- C. Tatewakii* Kudo, Jour. Coll. Agr. Sapporo 12: 61. 1923.—Isotype in Herb. Fac. Agr. Hokkaido Imp. Univ., lent to me through M. Tatewaki = *Hieracium*!
- C. tenuifolia* Willd., Sp. Pl. 3: 1606. 1804.—*Youngia tenuifolia* subsp. *typica* Babc. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 48. 1937.
- C. tenuifolia* Soland. et Banks, ex Lowe, Trans. Camb. Phil. Soc. 4: 24. 1831.—*Tolpis pectinata* fide I.K.
- C. tonkinensis* Gagnep., Bull. Soc. Bot. Fr. 6: 48. 1921.—*Launaea acaulis*!
- C. trichocarpa* Franch., Jour. de Bot. 9: 257. 1895.—*Sorosseris Gillii* subsp. *typica* (?) Stebbins, Mem. Torrey Bot. Club 19: 42. 1940.
- C. trichotoma* Moench., Meth. Suppl. 216. 1802.—*Tolpis coronopifolia* fide I.K.
- C. tsarongensis* (W. W. Smith) Anthony, Notes Bot. Gard. Edinb. 18: 194. 1934.—*Dubyaea tsarongensis* (W. W. Smith) Stebbins, Mem. Torrey Bot. Club 19: 24. 1940.
- C. tsarongensis* var. *chimiliensis* Anthony, Notes Bot. Gard. Edinb. 18: 194. 1934.—*Dubyaea chimiliensis* (W. W. Smith) Stebbins, Mem. Torrey Bot. Club 19: 24. 1940.
- C. umbellata* Bernh., Syst. Verz. Erf. 138. 1800.—*Hieracium umbellatum* fide I.K.
- C. umbrella* Franch., Jour. de Bot. 9: 225. 1895.—*Sorosseris umbrella* (Franch.) Stebbins, Mem. Torrey Bot. Club 19: 33. 1940.
- C. versicolor* Fisch., ex DC., Prod. 7: 151. 1838.—*Lactuca Fischeriana* fide I.K.
- C. virgata* Desf., Act. Soc. Hist. Nat. Par. 1: 37. 1792; Willd., Sp. Pl. 3: 1600. 1804.—*Tolpis virgata* fide DC.; confirmed in herb. Willd. (B).
- C. virgata* Lapeyr., Hist. Abr. Pl. Pyr. 483. 1813.—*Picris hieracioides* fide I.K.
- C. Wilsoni* Babc., Univ. Calif. Publ. Bot. 14: 331. 1928.—*Youngia Wilsoni* (Babc.) Babc. et Stebbins, op. cit. 79.
- C. yunnanensis* Babc., Univ. Calif. Publ. Bot. 14: 332. 1928.—*Youngia paleacea* subsp. *yunnanensis* (Babc.) Babc. et Stebbins, Carnegie Inst. Wash. Publ. No. 484: 71. 1937.

PLATES

PLATE 2

Crepis aurea (L.) Cass. *a*, subsp. *typica* Bab., type of Cassini (K); *b*, subsp. *lucida* (Ten.) Bab., type of Tenore (K); *c*, *d*, minor variants.

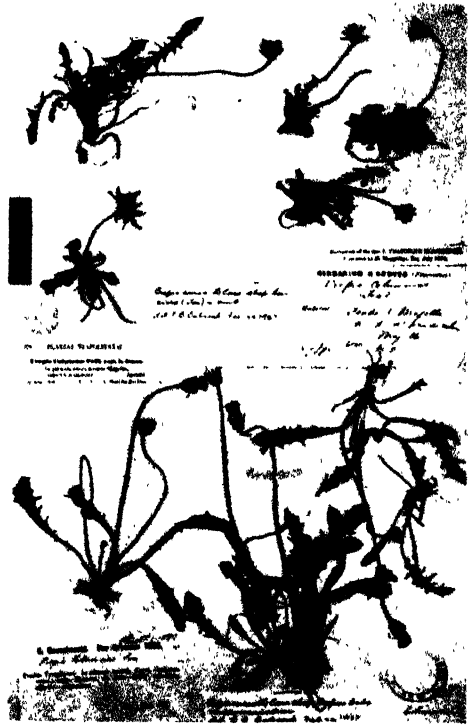
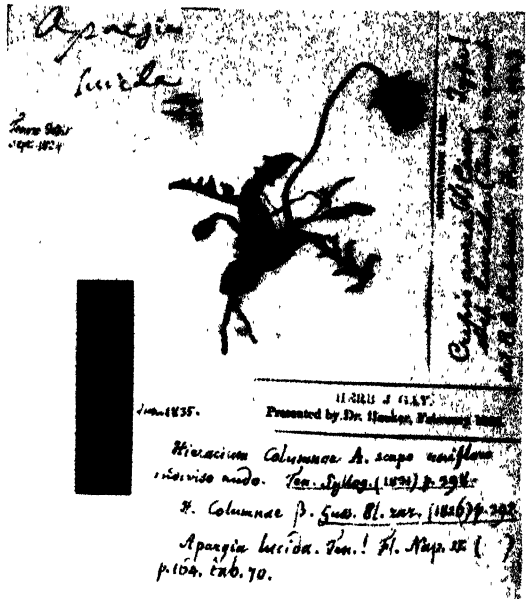


PLATE 3

Crepis chrysantha (Ledeb.) Froel. Authentic specimens of Ledebour and Turczaninow (DC).



PLATE 4

Crepis conyzaeifolia (Gouan) Dalla Torre. An unusually vigorous specimen in herb. Willd. no. 14753 (B).



PLATE 5

Crepis blattarioides (L.) Vill. *a*, an authentic specimen of Villar (Grenoble); *b*, a specimen closely similar in habit, leaves, and indumentum; *c*, a specimen with more coarsely dentate, strongly auriculate leaves; note the stout woody root bearing strong fibers.



PLATE 6

Crepis achyrophoroides Vatke. Isotype (US).



PLATE 7

Crepis biennis L. type (L).

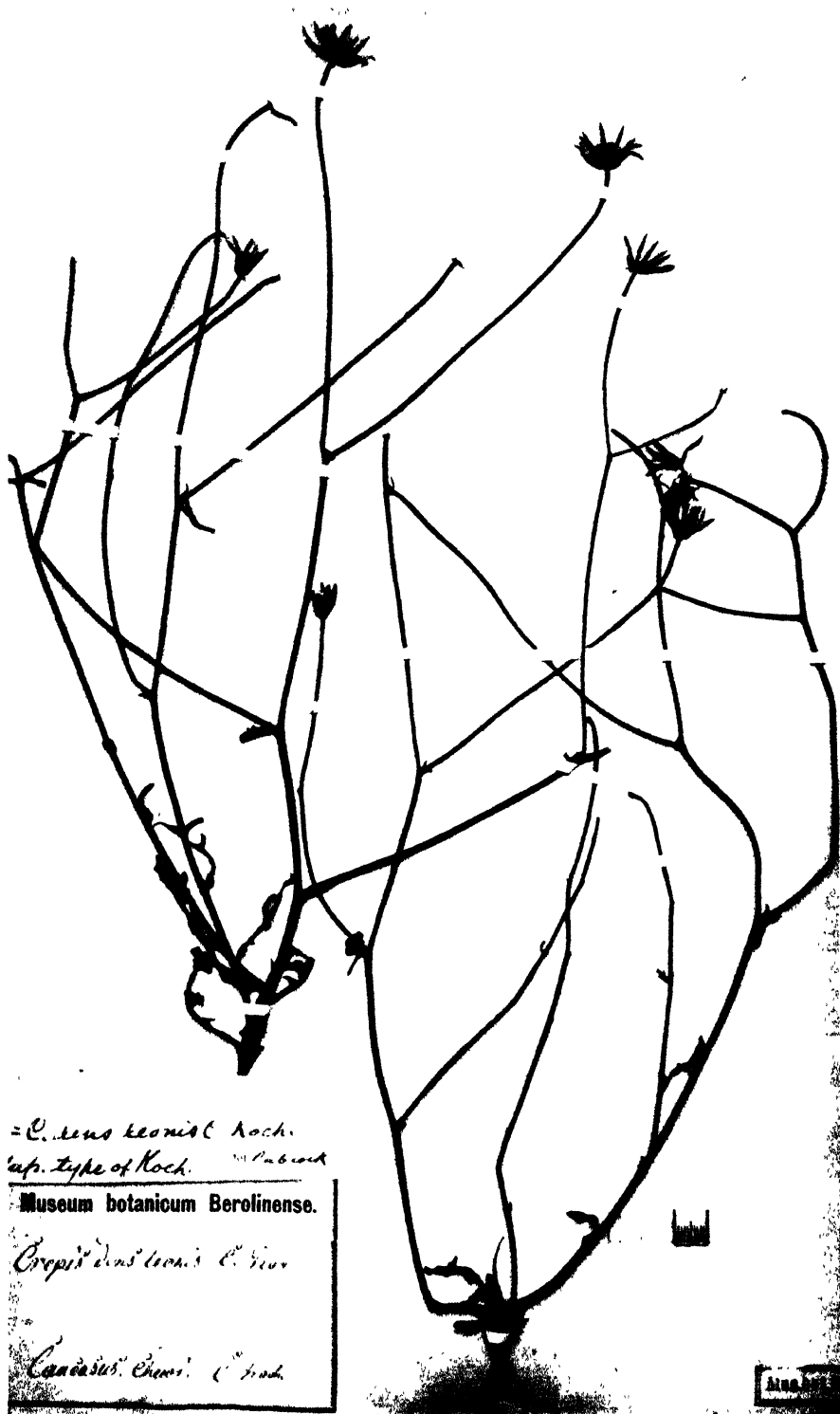


0 1 2 3 4 5 6 7 8 9 10

Centim.

PLATE 8

Crepis dens-leonis C. Koch. Isotype (B).



= *C. levis* Leonist Koch.
 var. type of Koch. not Cabanis

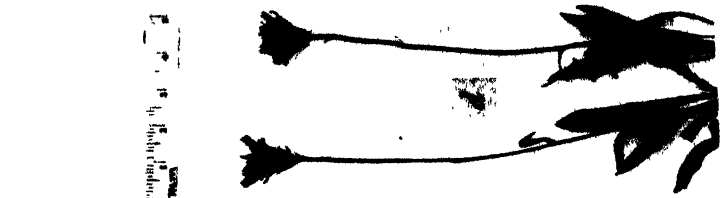
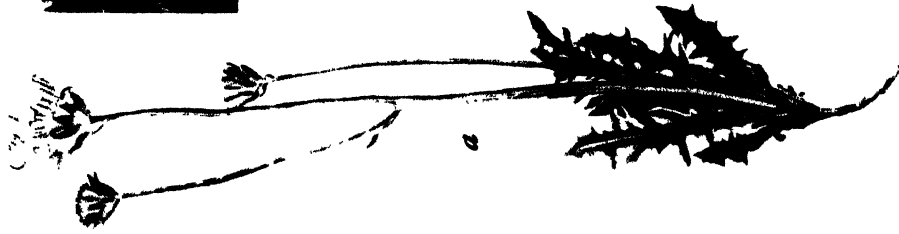
Museum botanicum Berolinense.

Crepis diastylon C. Hier.

Candollei Hier. C. Hier.

PLATE 9

Crepis crocea (Lamk.) Babe. and *Crepis oreades* Schrenk. *a-c*, *Crepis crocea* (Lamk.) Babe.; *d*, *Crepis oreades* Schrenk: *a*, *Hieracium croceum* Lamk., in Gmelin, Fl. Sib. II, tab. viii, f. 1; *b, c*, *H. croceum* Lamk., in Herb. DC. Prod. vii, 163-36 (DC); *d*, "*H. croceum* W." (DC). Inset, *C. crocea* in fruit in hort. genet. Calif. June 7, 1932.



Hydrocotyle ciliolata Wats.

Hydrocotyle ciliolata Wats.
1889, *Ann. Bot. Soc. Amer.* 6: 184.

Hydrocotyle ciliolata Wats.
1889, *Ann. Bot. Soc. Amer.* 6: 184.

Hydrocotyle ciliolata Wats.
1889, *Ann. Bot. Soc. Amer.* 6: 184.

PLATE 10

Crepis xylorrhiza Sch. Bip. *a*, type (PC); *b*, an authentic specimen, *Schimper 371* (P).



PLATE 11

Crepis flexuosa (DC.) Benth. *a, b*, typical fully developed plants;
c, d, younger plants which have not lost their caudical leaves.
Thompson in 1847 (K).

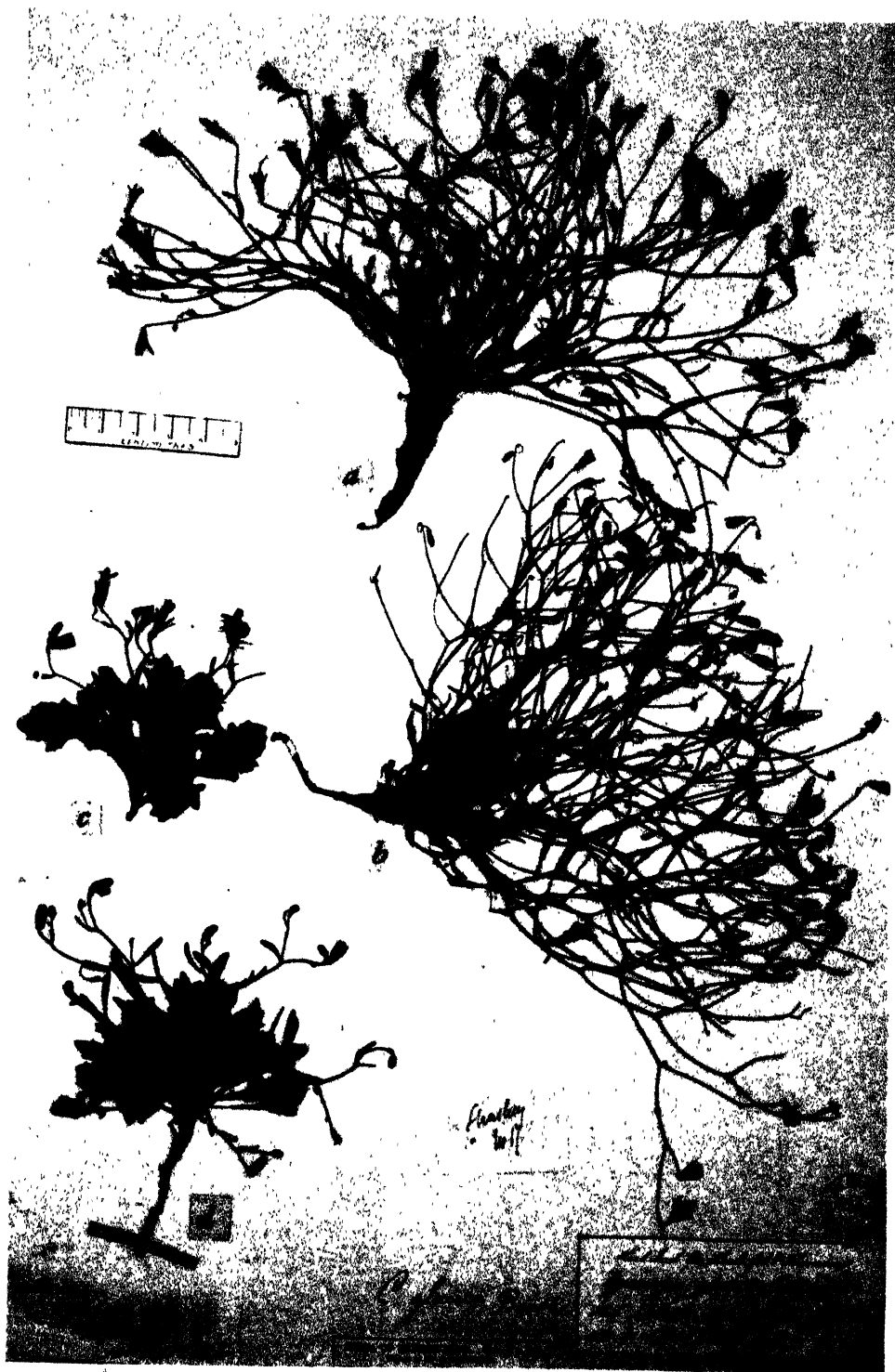


PLATE 12

Crepis Bungei Ledeb. Authentic specimens in herb. DC. Three collections, from left to right: ad fluv. Tineun, 1835, misit Turczaninoff, 1836; Baie. in uliginosis, 1830, misit Turczaninoff, 1833; in paludosis humidis ad ostium Kiachta, 1829, misit Turczaninoff à Irkoutsk, 1830. Cf. fig. 164.



PLATE 13

Crepis atribarba Heller subsp. *originalis* Bab. et Stebbins. *a*, an anomalous diploid form with small heads, exceptionally short achenes, and undetermined geographic range, *Eggleston 12869* (US); *b*, apm. *yakimensis* (*atribarba-acuminata*) *Piper 2737* (G) $2n = 88$ ♀; *c*, apm. *brevicarpa* (*atribarba-acuminata-modocensis* ♀) *St. John, Courtney, and Parker 3712* (WSC) $2n = 44$ ♀; *d*, related to apm. *sterilis* (*atribarba-acuminata-modocensis*) *Osterhout 3315* (Nev).

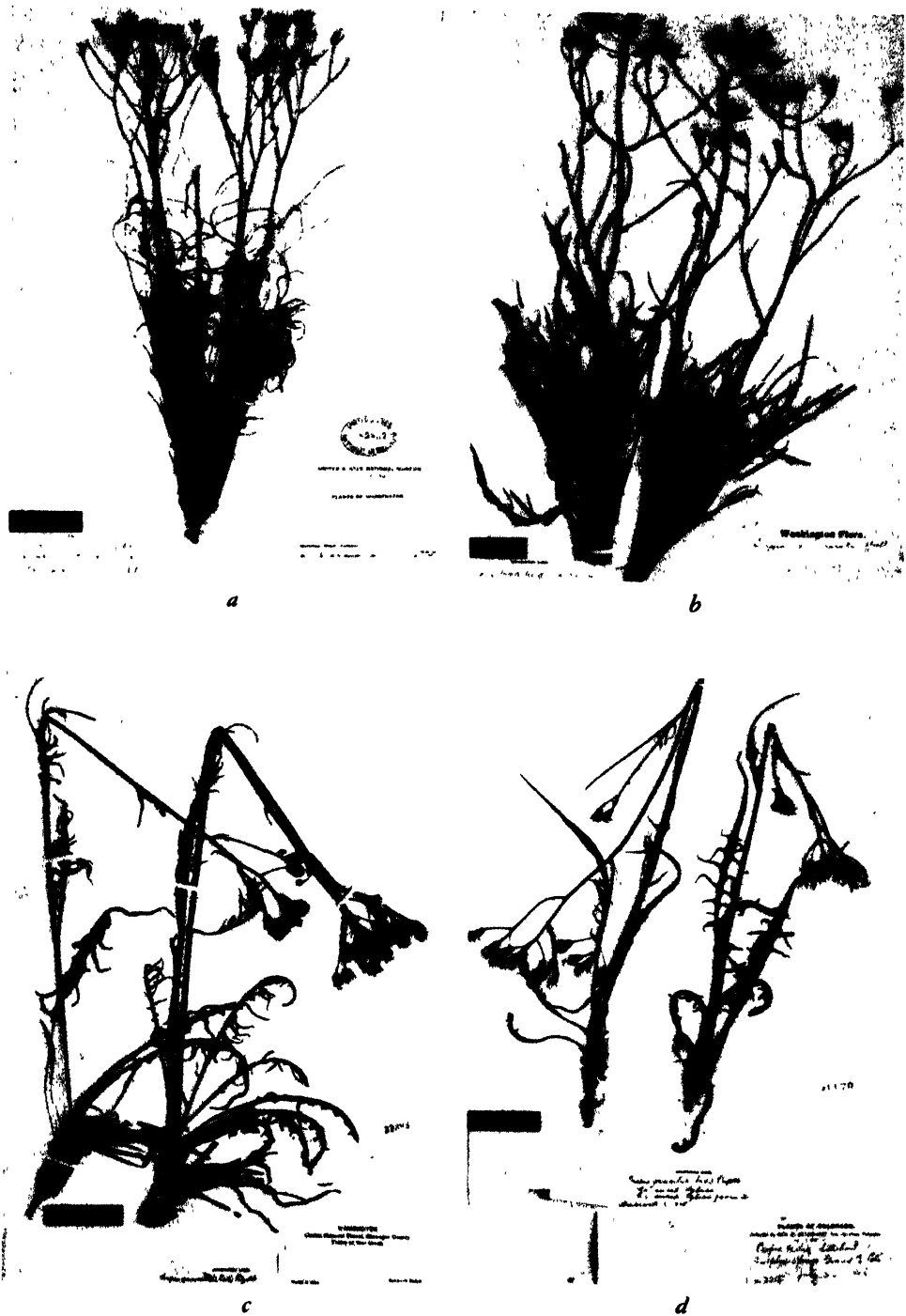


PLATE 14

Crepis lignea (Vaniot) Babe. and *Crepis rigescens* Diels. *a-d*, *f*, *g*, *Crepis lignea* (Vaniot) Babe.; *e*, *Crepis rigescens* Diels: *a*, type of *Lactuca lignea* Vaniot (E), *b*, m.v., 2, and *c*, m.v. 3 (UC); *d*, m.v. 4, and *e*, *C. rigescens* (US); *f*, m.v. 5, and *g*, m.v. 7 (UC).

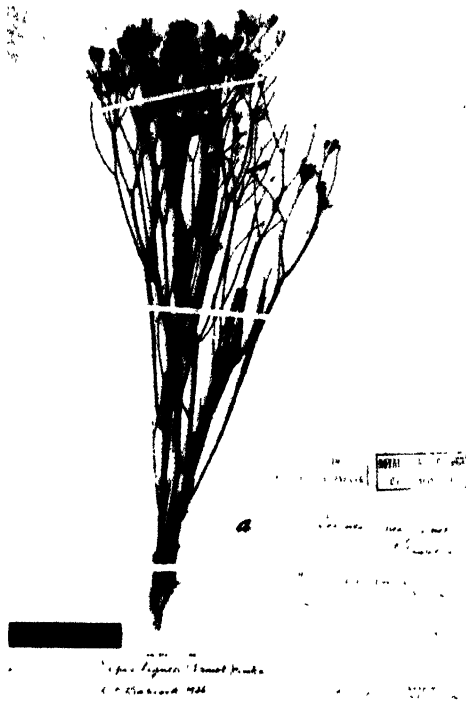
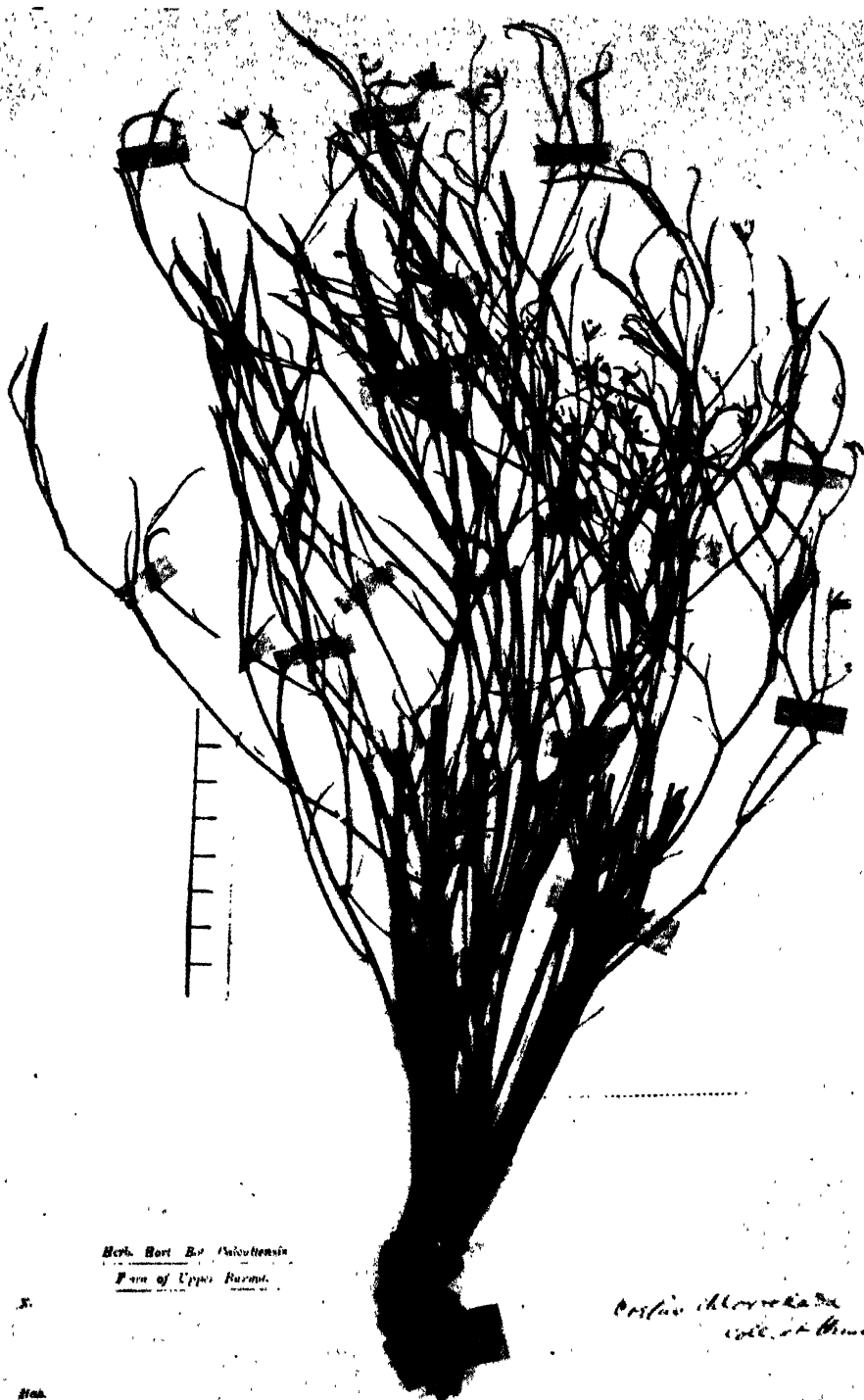


PLATE 15

Crepis chloroclada Coll. et Hemsl. Type (K).



Herb. Hort. Bot. Calcuttensis
Para of Upper Burma.

Cyperus chlorostachyus
Willd. ex Thunb.

S.

Herb.

all

late

1888. General Dept. C. A.

PLATE 16

Crepis alpina L. *a*, type (L); *b*, a robust specimen collected by Heldreich (B); *c*, *Bornmuller 206B* (B) m.v. 2; *d*, a tall plant from Persia collected by C. Koch (B) m.v. 3 = *Barkhausia elata* Koch.

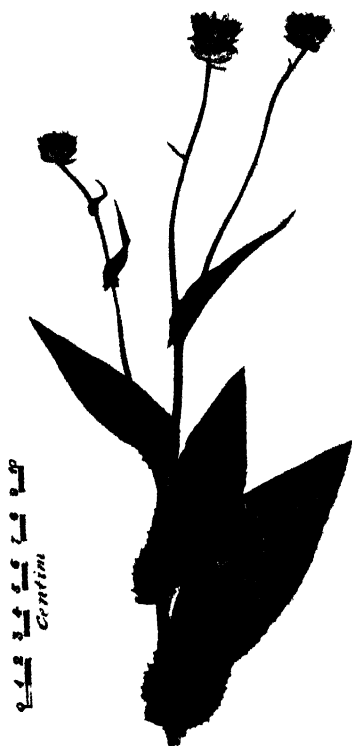


PLATE 17

Crepis foetida L. *a*, subsp. *vulgaris* (Bisch.) Babe., type (L);
b-d, *Ross 158* (G); *b* and *c* = m.v. 1, *d* = m.v. 2.



PLATE 18

Crepis foetida L. *a*, *b*, subsp. *rhoadifolia* (Bieb.) Schinz et Keller; *c*, subsp. *vulgaris* m.v. 47 = *Crepis fallax* Boiss. (Bo); *d*, subsp. *commutata* (Spr.) Bab.: *a*, Bornmuller 393 (K); *b*, Aucher-Eloy in 1837 (DC); *c*, type of *C. fallax* Boiss. (Bo); *d*, Bornmuller in 1910 (Bornm) as *C. brachypappa*.



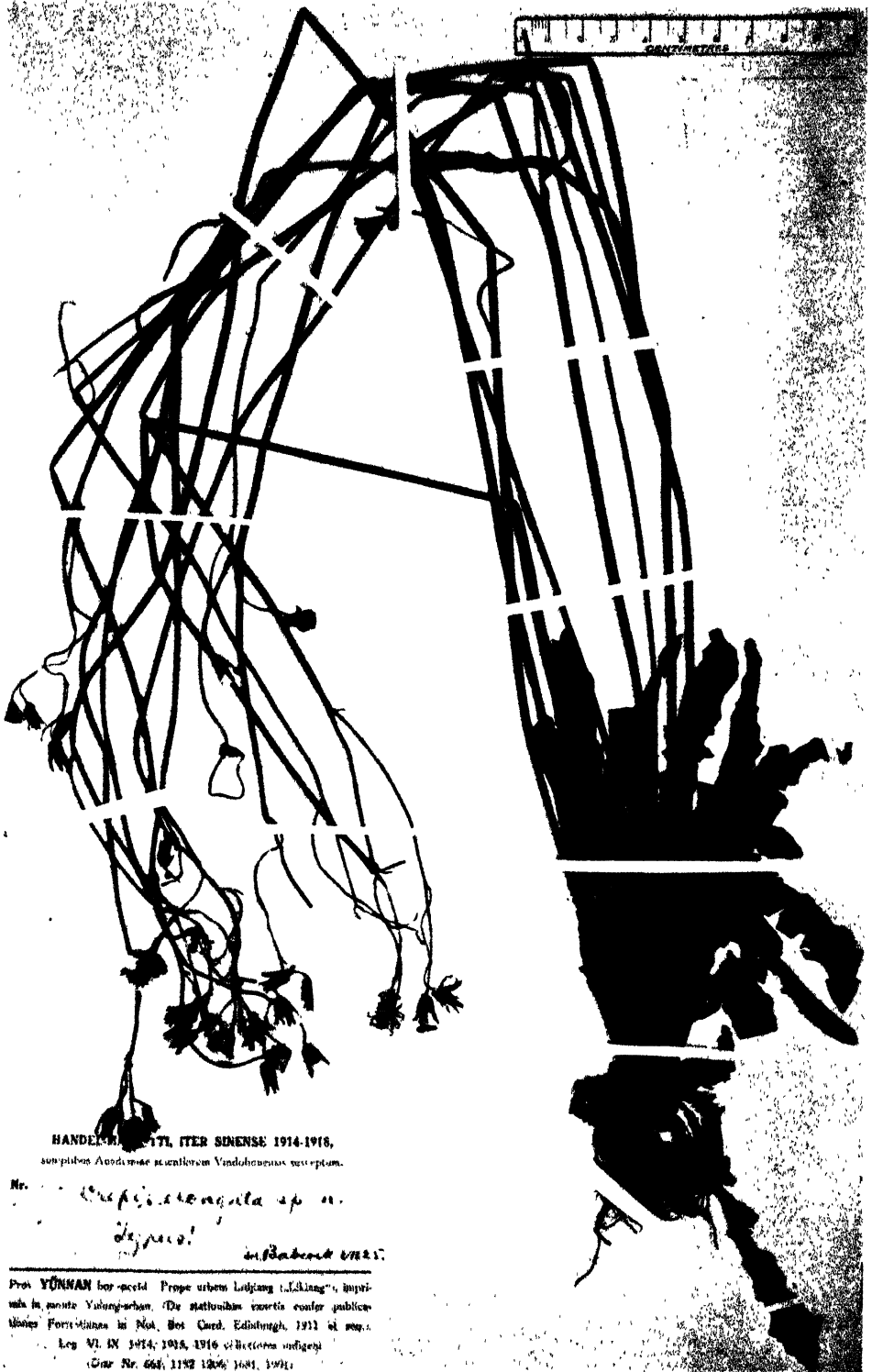
PLATE 19

Crepis Gmelini (L.) Tausch. *a*, type of Linné (L) (note that the leaf shown on the right does not belong to this species); *b*, type of Tausch (PD); *c*, Gmelin's figure of *Hieracium Gmelini* L. in Fl. Sib. II, t. viii, f. 2; *d*, type of *Crepis multicaulis* var. *ochotensis* DC. (DC); *e*, *Turczaninoff* in 1835 (K). Cf. fig. 221.



PLATE 20

Crepis elongata Babe. Type (MW)



HANDEL, 1911, ITER SINENSE 1914-1916,
 solum pilosum Anodumae aculeosum Vindobonensis receptum.

Nr. *Epipactis atrorubens* sp. n.
Epipactis
infidabens 1914.

Pro: YÜNNAN her. aced. Prope urbem Lüchiang (Lüchiang), impri-
 ma in monte Yüling-shan. De statuibus exerts. conser. publicae
 Chinae Fort. Sinensis in Not. Bot. Gard. Edinburgh, 1913 et seq.
 Leg. VI. IN 1914, 1915, 1916 et 1917. (Gard. Nr. 664, 1152 1206 1681, 1911)

PLATE 21

Crepis multicaulis Ledeb. subsp. *genuina* (Rgl.) Bab. *a*, Altai, *Bunge* (DC), probably an isotype; *b*, Turkestan, *Regel* in 1877 (K); *c*, Norway, *Fries* in 1864 (FM); *d*, Kashmir, *Stewart 6416* (NY).



PLATE 22

Crepis multicaulis Ledeb. subsp. *congesta* (Rgl.) Babe. All from Kashmir. *a*, *Falconer 3029, 3646* (K), which agree with Regel's description; *b*, *Stoliczka* in 1865 (K), type of *C. Stoliczka* C. R. Clarke; *c*, *Duthie 11605* (K); *d*, *Clarke 29871* (K).

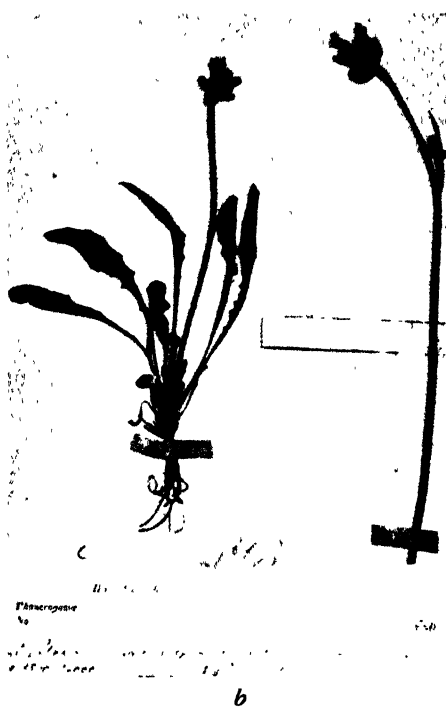
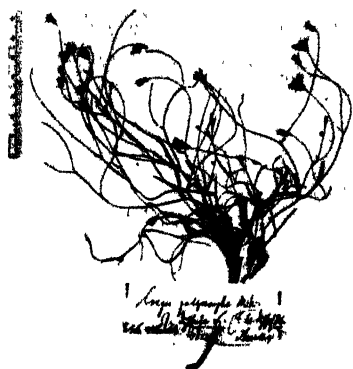


PLATE 23

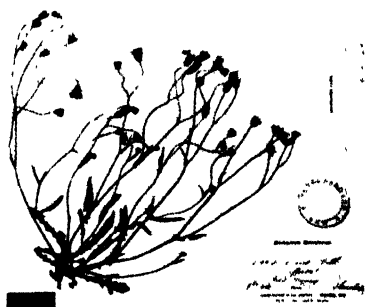
Crepis nicaeensis Balb. *a*, type (Torino) ; *b*, *Bubela* in 1883 (K) ;
c, *Ausserdorfer 3411* (Minn) ; *d*, left, *Koch* in 1838, right, *Reuter*
in 1838 (K). Note variations in outline of leaves.

PLATE 24

Crepis capillaris (L.) Wallr. *a*, type of *C. diffusa* DC. and *C. polymorpha* var. *diffusa* Wallr. Wallroth in 1822 (DC) m.v. 1; *b*, Blanchet in 1864 (K) m.v. 1; *c*, Bourgeau 309 (K) m.v. 1; *d*, Lacaita 498 (BM-L 28630) m.v. 1; *e*, J. Ball in 1848 (G) m.v. 2; *f*, type of *C. polymorpha* var. *stricta* Wallr., Wallroth in 1822 (DC) m.v. 7; *g*, Bourgeau 310 (K) m.v. 5; *h*, Nelson 1246 (G) m.v. 10.



a



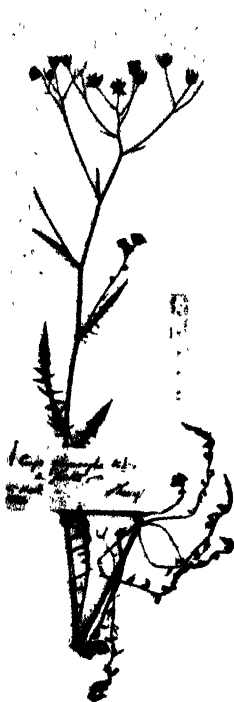
b



d



b



f



c



e

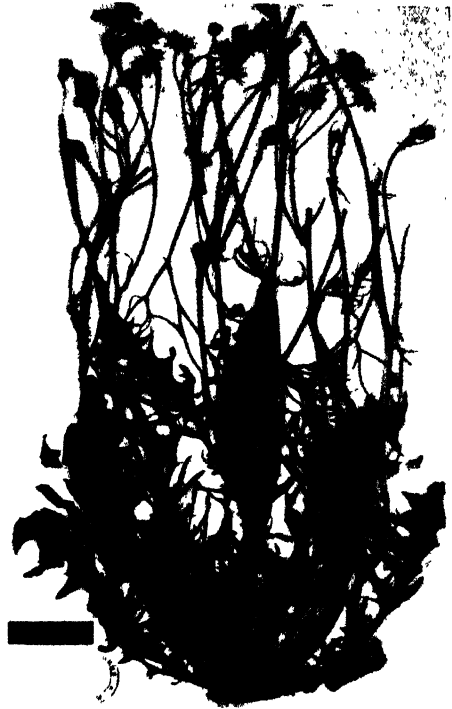
g

PLATE 25

Crepis capillaris (L.) Wallr. *a*, *Babcock and Navashin 188B*
(UC) m.v. 3; *b*, *Bromfield* in 1845 (K) m.v. 4; *c*, *Schultz* in 1837
(K) m.v. 6; *d*, *Hubbard 712* (K) m.v. 8.



a



b



c



d

PLATE 26

Crepis insignis Bab. Type (DL). Cf. fig. 245.



Mesopotamia HABITAT
Plantago syriaca borealis
H. B. COCKFIELD

1888.

Dr. C. A. Hammel
2000 - 4700 ft

Crepis insignis sp. n.
Lepus.

Dr. C. A. Hammel, 16.VI.23



PLATE 27

Crepis Salzmannii Bab. Type (K). Cf. fig. 254.



ANNOUATION LABEL

Crepis Salzmännii sp. nov.
TYPE

Christensen, det.
Dec. 22

PLATE 28

Crepis Bourgeani Bab. *a*, type (P); *b*, *Gros* in 1925 (Bar) m.v. 1; *c*, *Gros* in 1925 (UC) m.v. 2; *d*, *Hooker* in 1871 (K) m.v. 3.



a



FORM 1

b



FORM 2

c



FORM 3

d

PLATE 29

Crepis Balluana Babc. Type (K).



PLATE 30

Crepis vesicaria L. subsp. *typica* (Fiori) Babe. *a*, type (L.); *b*,
C. raphanifolia Willd. in herb. Willd. (B).



1 2 3 4 5 6 7 8 9 10
Centim.
a



Cephus occidentalis L.
spp. *lyfuen* Ktze.
A. T. & B. Babcock
1915

Cephus occidentalis
L.
b

PLATE 31

Crepis vesicaria L. subsp. *myriocephala* (Coss. et Durieu) Balc.
Warrior in 1873 (G).



Portulaca O. S. M. M.
P. M. M.
Portulaca megalocephala Coss. et al. 1914

PLATE 32

Crepis vesicaria L. subsp. *taraxacifolia* (Thuill.) Thell. *a*, *C. intybacca* Brot., Phytograph. Lusit. 1: t. 26 = m.v. 51; *b*, *Barkhausia laciniata* Lowe, Lemann in 1825 (K) m.v. 52; *c*, *B. laciniata* var. *pinnatifida* Lowe, Bornmuller 878 (PA) m.v. 52; *d*, *B. laciniata* var. *integrifolia* Lowe, Bornmuller 878b (PA) m.v. 53.



a



b



c



d

PLATE 33

Crepis vesicaria L. subsp. *andryaloides* (Lowe) Bab. *a*, type of *Barkhausia hieracioides* Lowe (K); *b*, m.v. 72, which approaches m.v. 71; *c*, m.v. 70 = *C. dubia* (Lowe) F. Schultz (G); *d*, m.v. 71 = *C. comata* (Lowe) Banks et Sol. (Bo).



a



b



c



d

PLATE 34

Crepis vesicaria L. subsp. *proleptica* Bab. Type (K)



PLATE 35

Crepis vesicaria L. subsp. *congenita* Bab. Type (Po).



U. S. BAKER HERBARIUM
17721
POMONA, CALIF.

Crepis virens L.
subsp. *complanata* (L.)

Crepis glauca (L.)
Gussone & Kerner.
L. Müller.

PLATE 36

Crepis Rueppellii m.v. 1. "*Schimper*, pl. Abyss., E. Hohenacker
no. 217" (G) det. Hochst., as *Crepis* (*Barkhausia*) *adenothrix*
Sch. Bip.



INDEX TO EXSICCATAE CITED

The specimens are cited by the collector's number in italics, when available, otherwise by the year of collection. In parentheses are given the numbers of the species, a species number being followed by a small letter when designating a subspecies. To facilitate the annotation of herbarium specimens, the numbered list of species and subspecies, the latter in italics, here precedes the collectors, collector's numbers, and numbers of the species.

List of Species and Subspecies

1. *C. sibirica* L.
2. *C. geracioides* Hausskn.
3. *C. viscidula* Froel.
4. *C. paludosa* (L.) Moench
5. *C. kashmirica* Babc.
6. *C. pygmaea* L.
 a. typica Babc.
 b. anachoretica Babc.
7. *C. terglouensis* (Hacq.) A. Kern.
8. *C. rhaetica* Hegetschw.
9. *C. Jacquini* Tausch
10. *C. hokkaidoensis* Babc.
11. *C. aurea* (L.) Cass.
 a. typica Babc.
 b. lucida Babc.
12. *C. chrysantha* (Ledeb.) Froel.
13. *C. polytricha* (Ledeb.) Turcz.
14. *C. albiflora* Babc.
15. *C. dioritica* Schott. et Kotschy
16. *C. lapsanoides* [lampsanoides]
 (Gouan) Tausch
17. *C. smyrnaea* DC.
18. *C. lyrata* (L.) Froel.
19. *C. mollis* (Jacq.) Asch.
20. *C. willemetioides* Boiss.
21. *C. hierosolymitana* Boiss.
22. *C. montana* Urv.
23. *C. Mungierii* Boiss.
24. *C. pontana* (L.) Dalla Torre
25. *C. conyzaefolia* (Gouan) Dalla Torre
26. *C. blattarioides* (L.) Vill.
27. *C. albida* Vill.
 a. typica Babc.
 b. asturica (Lacaita et Pau) Babc.
 c. Grosii (Pau) Babc.
 d. scorzoneroideis (Rouy) Babc.
 e. macrocephala (Willk.) Babc.
 f. longicaulis Babc.
28. *C. achyrophoroides* Vatke
29. *C. elymaitica* Bornm.
30. *C. kilimandscharica* O. Hoffm.
31. *C. keniensis* (R. E. Fr.) Babc.
32. *C. alpestris* (Jacq.) Tausch
33. *C. suffruticosa* Babc.
34. *C. iringensis* Babc.
35. *C. meruensis* Babc.
36. *C. cameroonica* Babc.
37. *C. Schultzii* (Hochst.) Vatke
38. *C. carbonaria* Sch. Bip.
39. *C. Ellenbeckii* R. E. Fr.
40. *C. urundica* Babc.
41. *C. hypochaeridea* (DC.) Thell.
 a. genuina (Thell.) Babc.
 b. rhodesica Babc.
 c. brevicaulis Babc.
42. *C. chirindica* S. Moore
43. *C. congoensis* Babc.
44. *C. caudicalis* Babc.
45. *C. Newii* Oliver et Hiern
 a. typica Babc.
 b. Greenwayi Babc.
 c. bumbensis (Hiern) Babc.
 d. kundensis Babc.
 e. nyasensis Babc.
 f. itakensis Babc.
46. *C. scaposa* R. E. Fr.
 a. typica Babc.
 b. eximia Babc.
 c. afromontana (R. E. Fr.) Babc.
 d. tarazaciformis (R. E. Fr.) Babc.
47. *C. glandulosissima* R. E. Fr.
48. *C. ugandensis* Babc.
49. *C. Swynnertonii* S. Moore
50. *C. subscaposa* Collett et Hemsl.
51. *C. simulans* S. Moore
52. *C. Gossweileri* S. Moore
53. *C. Friesii* Babc.
54. *C. Mildbraedii* Babc.
55. *C. Bruceae* Babc.
56. *C. tingitana* Salz.
57. *C. leontodontoides* All.

58. *C. suberostris* Coss. et Durieu
 59. *C. Strausii* Bornm.
 60. *C. darvasica* H. Krasch.
 61. *C. songorica* (Kar. et Kir.) Babe.
 62. *C. sonchifolia* (M. Bieb.) C. A. Mey.
 63. *C. ciliata* C. Koch
 64. *C. biennis* L.
 65. *C. pannonica* (Jacq.) K. Koch
 66. *C. latialis* Sebast.
 67. *C. bertisceae* Jav.
 68. *C. chondrilloides* (Scop.) Jacq.
 69. *C. bupleurifolia* (Boiss. et Kotschy) Freyn et Sint.
 a. typica Babe.
 b. meletonis (Hand.-Mazz.) Babe.
 70. *C. auriculaefolia* Sieber
 71. *C. Baldaccii* Hal.
 72. *C. turcica* Degen et Bald.
 73. *C. Pantocseckii* (Vis.) Markg.
 74. *C. Triasii* (Camb.) Fries
 75. *C. Raulini* Boiss.
 76. *C. albanica* (Jav.) Babe.
 77. *C. macropus* Boiss. et Heldr.
 78. *C. oporinoides* Boiss.
 79. *C. dens-leonis* C. Koch
 80. *C. Sibthorpiana* Boiss. et Heldr.
 81. *C. khorassanica* Boiss.
 82. *C. incana* Sibth. et Sm.
 83. *C. taygetica* Babe.
 84. *C. turcomanica* H. Krasch.
 85. *C. Guioliana* Babe.
 86. *C. crocifolia* Boiss. et Heldr.
 87. *C. athoa* Boiss.
 88. *C. Schachtii* Babe.
 89. *C. pinnatifida* (Willd.) Froel.
 90. *C. bithynica* Boiss.
 91. *C. oreades* Schrenk
 92. *C. crocea* (Lamk.) Babe.
 93. *C. tenerrima* (Sch. Bip.) R. E. Fr.
 94. *C. xylorrhiza* Sch. Bip.
 95. *C. Hookeriana* J. Ball
 96. *C. Faureliana* Maire
 97. *C. Robertioides* Boiss.
 98. *C. heterotricha* DC.
 a. typica Babe.
 b. lobata Babe.
 99. *C. armena* DC.
 a. typica Babe.
 b. longibractea Babe.
 100. *C. demavendi* Bornm.
 101. *C. abyssinica* Sch. Bip.
 102. *C. corniculata* Rgl. et Schmalh.
 103. *C. alaica* H. Krasch.
 104. *C. flexuosa* (DC.) Benth.
 105. *C. naniforma* Babe.
 106. *C. lactea* Lipsch.
 107. *C. nana* Richards.
 a. typica Babe.
 b. ramosa Babe.
 108. *C. elegans* Hook.
 109. *C. gymnopus* Koidzumi
 110. *C. praemorsa* (L.) Tausch
 111. *C. incarnata* (Wulf.) Tausch
 112. *C. ircutensis* Babe.
 113. *C. Bungei* Ledeb.
 114. *C. tectorum* L.
 115. *C. monticola* Coville
 116. *C. occidentalis* Nutt.
 a. typica Babe. et Stebbins
 b. costata (Gray) Babe. et Stebbins
 c. pumila (Rydb.) Babe. et Stebbins
 d. conjuncta (Jepson) Babe. et Stebbins
 117. *C. Bakeri* Greene
 a. typica Babe. et Stebbins
 b. Cusickii (Eastw.) Babe. et Stebbins
 c. idahoensis Babe. et Stebbins
 118. *C. modocensis* Greene
 a. typica Babe. et Stebbins
 b. subacaulis (Kell.) Babe. et Stebbins
 c. rostrata (Cov.) Babe. et Stebbins
 d. glareosa (Piper) Babe. et Stebbins
 119. *C. pleurocarpa* Gray
 120. *C. acuminata* Nutt.
 a. typica Babe. et Stebbins
 b. pluriflora Babe. et Stebbins
 121. *C. atribarba* Heller
 a. originalis Babe. et Stebbins
 b. typica Babe. et Stebbins
 122. *C. intermedia* Gray
 123. *C. barbigera* Leiberg
 124. *C. runcinata* Torr. et Gray
 a. typica Babe. et Stebbins
 b. hispidulosa (Howell) Babe. et Stebbins
 c. glauca (Nutt.) Babe. et Stebbins
 d. Barberi (Greenm.) Babe. et Stebbins
 e. imbricata Babe. et Stebbins

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 126. *C. sahendi* Boiss. et Buhse
 127. *C. purpurea* (Willd.) M. Bieb.
 128. *C. elbrusensis* Boiss.
 129. *C. frigida* (Boiss.) Bab.
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 131. *C. Phoenix* Dunn
 132. *C. Bodinieri* Lev.
 133. *C. rigescens* Diels
 a. typica Bab.
 b. lignescens Bab.
 134. *C. lignea* (Vaniot) Bab.
 135. *C. chloroclada* Collett et Hemsl.
 136. *C. Reuteriana* Boiss.
 a. typica Bab.
 b. Eigiana Bab.
 137. *C. palaestina* (Boiss.) Bornm.
 138. *C. pulchra* L.
 a. typica Bab.
 b. africana Bab.
 c. turkestanica Bab.
 139. *C. amanica* Bab.
 140. *C. Stojanovii* Georg.
 141. *C. pterothecoides* Boiss.
 142. *C. alpina* L.
 143. *C. syriaca* (Bornm.) Bab.
 144. *C. rubra* L.
 145. *C. foetida* L.
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 b. rhoeadifolia (M. Bieb.) Schinz et Keller
 c. commutata (Spr.) Bab.
 146. *C. Schimperii* Sch. Bip.
 147. *C. Kotschyana* Boiss.
 148. *C. eritreënsis* Bab.
 149. *C. Thomsonii* Bab.
 150. *C. tybakiensis* Vierh.
 151. *C. tibetica* Bab.
 152. *C. Gmelini* (L.) Tausch
 153. *C. elongata* Bab.
 154. *C. multicaulis* Ledeb.
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 155. *C. sancta* (L.) Bab.
 a. nemausensis (Gouan) Thell.
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 c. obovata (Boiss. et Noë) Bab.
 156. *C. patula* Poir.
 157. *C. Dioscoridis* L.
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 b. argolica Bab.
 c. tiryntica Bab.
 d. tubaeformis Bab.
 158. *C. multiflora* Sibth. et Sm.
 159. *C. Zacintha* (L.) Bab.
 160. *C. nicaeënsis* Balb.
 161. *C. capillaris* (L.) Wallr.
 162. *C. parviflora* Desf.
 163. *C. insignis* Bab.
 164. *C. neglecta* L.
 165. *C. corymbosa* Ten.
 166. *C. fuliginosa* Sibth. et Sm.
 167. *C. cretica* Boiss.
 168. *C. apula* (Fiori) Bab.
 169. *C. Suffreniana* (DC.) Lloyd
 170. *C. spathulata* Guss.
 171. *C. Salzmannii* Bab.
 172. *C. Clausonis* (Pomel) Batt. et Trab.
 173. *C. Fontiana* Bab.
 174. *C. Bourgeauii* Bab.
 175. *C. canariensis* (Sch. Bip.) Bab.
 176. *C. divaricata* (Lowe) F. Schultz
 177. *C. Noronhaea* Bab.
 178. *C. Balliana* Bab.
 179. *C. libyca* (Pamp.) Bab.
 180. *C. Claryi* Batt.
 181. *C. vesicaria* L.
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 182. *C. Marschallii* (C. A. Mey.) F. Schultz
 183. *C. juvenalis* (Delile) F. Schultz
 184. *C. aculeata* (DC.) Boiss.
 185. *C. amplexifolia* (Godr.) Willk.
 186. *C. atheniensis* Bab.
 187. *C. aspera* L.
 188. *C. setosa* Hall. f.
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